CONTRIBUTION OF AGRICULTURAL LAND USES TO BIRD CONSERVATION: A CASE STUDY OF ECOSYSTEM SERVICE PROVISIONING

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by

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This dissertation of María Alejandra Martínez Salinas, submitted for the Degree of Doctorate of Philosophy with a Major in Natural Resources and titled "**Contribution of agricultural land uses to bird conservation: a case study of ecosystem service provisioning,**" has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Understanding the contribution of agricultural land uses to biodiversity conservation is of utmost importance. With 38% of earth's ice free land surface covered by crops and pastures, studying and understanding the potential conservation value of these lands is critical for the future of conservation strategies, particularly in biodiversity conservation hotspots such as Central America.

My research focused on understanding the contribution of different agricultural land uses and a forest fragment to bird conservation in a Costa Rican landscape. The study region is located at the heart of the Volcanica Central Talamanca Biological Corridor (VCTBC), a national conservation strategy aiming at reconnecting the Volcanica Central and the Talamanca Mountain Ranges. Chapter 1 and Chapter 2 are based on seven years of bird capture data produced by long-term mist-netting stations operating in eight different land uses, seven agricultural and a forest fragment. Chapter 1 comprises lessons learned during seven years of mist-netting efforts in eight land uses following a management intensity gradient. Chapter 2 focuses on bird community stability, stability understood as no changes from year to year in mean species richness and abundance of either the total population, or of resident and migratory species over a seven year period. Chapter 3 is based on an experimental study focusing on the effect of bird species in the suppression of the Coffee Berry Borer (*Hypothenemus hampei*), one of the most detrimental coffee pests worldwide.

Results from our research highlights the importance of including agricultural land uses in biodiversity conservation planning. Agroforestry systems particularly showed potential for bird conservation in agricultural landscapes while fostering stable bird communities that are closer in composition to our reference forest fragment. Additionally, our results also showed that our landscape is capable of supporting bird species providing important pest control services. Finally, despite the value of agricultural land uses our results also highlight that our forest fragment fosters unique bird communities when compared to agricultural lands. Conservation planning at the landscape level should considered the uniqueness of these habitats and integrate efforts to conserve forests and managed agricultural lands for biodiversity conservation, particularly in these human-dominated landscapes.

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Dedication

Con amor y admiración para

Róger

Mamá, Papá, Elisa y Rommel

Renata y Lucas… para que nunca menosprecien

“la importancia de la guerra de las flores y los corderos”

y para que cuando sean adultos

una parte de ellos sea residente permanente del asteroide B612

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Chapter 1

Chapter 1. Lessons learned from long-term bird mist-netting stations in agricultural land uses in Costa Rica: implications to conservation and management

Abstract

Knowledge about tropical bird species persisting in agricultural land uses is essential to support management interventions. Mist-netting has long been recognized as an important monitoring technique in the study of avian populations. We have been running mist-netting stations in different agricultural and a forest land use since the year 2008, and we present here results and lessons learned from the first seven years of sampling. Land uses monitored are representatives of those predominant within the Volcanica Central Talamanca Biological Corridor (VCTBC) in Costa Rica. Using captured data we analyzed information about species richness, diversity indices, age structure and sex distribution across land uses, we then discussed recapture rates and captures of forest dependent species in agricultural land uses, finally we present information about bird functional traits. Results from our long-term mist-netting efforts show that agroforestry systems supports high species richness, uniformly distributed communities, high species diversity and low dominance as well as the greater number of expected species across land uses. Additionally, agroforestry systems such as live fences revealed fostering diverse bird communities as well as enabling forest dependent bird species dispersal through pasture lands. We were also able to collect functional trait measures for over one hundred bird resident species, this latter in an effort to make this information public and help advance studies of functional ecology on mobile organisms. Establishment and operation of long-term mist-netting stations particularly in the American tropics is crucial

to narrow the knowledge gap about most tropical bird species persisting in agricultural landscapes.

Keywords: Ornithology, bird banding, agroforestry systems, bird functional traits, agricultural landscapes, tropical ecosystems

Resumen

El conocimiento sobre especies de aves que persisten en usos de suelo agrícolas es esencial para informar acciones de manejo. Las estaciones de anillamiento son reconocidas como una importante herramienta en el monitoreo de poblaciones de aves silvestres. Desde el año 2008, hemos corrido estaciones de anillamiento en diferentes usos de suelo agrícola y un fragmento de bosque. Presentamos aquí resultados y lecciones aprendidas con base en los primeros siete años. Los usos de suelo monitoreados corresponden a usos predominantes dentro del Corredor Biológico Volcánica Central Talamanca (CBVCT) en Costa Rica. Utilizamos datos de capturas para analizar información relativa a riqueza de especies, índices de diversidad, y estructura de edades y sexos en los usos de suelo estudiados. También discutimos tasas de recapturas y capturas de especies dependientes de bosque en usos de suelo agrícolas, finalmente presentamos información sobre rasgos funcionales de aves. Resultados de nuestras estaciones de monitoreo muestran que los sistemas agroforestales albergan una alta riqueza de especies, comunidades equitativas, alta diversidad de especies y baja dominancia así como altos número de especies esperadas en comparación con los otros usos de suelo. Sistemas agroforestales como cercas vivas también revelaron albergar una diversa comunidad de aves, además de facilitar el movimiento de especies dependientes de bosque a través de pasturas.

Colectamos rasgos funcionales de más de cien especies de aves tropicales, en un esfuerzo por contribuir al avance de estudios de ecología funcional en organismos móviles. El establecimiento y operación a largo plazo de estaciones de anillamiento, particularmente en los trópicos americanos, es crucial para estrechar el vacío de información sobre la mayoría de especies de aves tropicales que aún persisten en paisajes agrícolas.

Palabras claves: Ornitología, anillamiento, sistemas agroforestales, rasgos funcionales, paisajes agrícolas, ecosistemas tropicales

Introduction

Mist-netting has long been recognized as an important monitoring technique in the study of avian populations (Ralph et al. 1993, Dunn and Ralph 2004). Through the use of mist-nets, researchers can obtain information related to population demographics (Latta et al. 2012, Amrhein et al. 2012, Rushing et al. 2016), including estimation of productivity and survival (DeSante et al. 2009, Ruiz-Gutierrez et al. 2012, Wolfe et al. 2015) which are essential characteristics determining population viability. Methods of capture-recapture also facilitate the collection of information related to overwintering strategies (Ruiz-Gutierrez et al. 2016), community stability (Osenkowski et al. 2012, Faaborg et al. 2013), habitat use and resource selection (Johnson et al. 2006, Ruiz-Gutierrez et al. 2010, Wolfe et al. 2014, Sekercioglu et al. 2015), changes in species composition through time (Mestre et al. 2013, Blake and Loiselle 2016), species movement (Neuschulz et al. 2013) and effects of important diseases such as the West Nile Virus (George et al. 2016). Animal handling via mist-netting also makes possible to collect tissue samples for DNA extractions (Karp et al. 2013, Ruegg et

al. 2014) and stable isotopes analysis (Fraser et al. 2008), and to evaluate variables such as body condition (Colorado and Rodewald 2016) and molt patterns (Ryder and Wolf 2009). Much of this information would be extremely difficult or impossible to obtain without the capturing of individuals through mist-netting protocols.

Morphological traits are amongst the valuable information that can be collected in mist-netting stations. The study of traits has been increasingly recognized as crucial in the understanding of species and community responses to environmental gradients (Ackerly and Cornwell 2007) and their role in ecological processes and functions associated with ecosystem service delivery (Díaz and Cabido 2001, Petchey and Gaston 2006, Barbaro et al. 2014). Capture and handling of wild animals provide with the unique opportunity to measure physical characteristics that can then be used to applied functional diversity approaches based on functional trait values (Philpott et al. 2009, Flynn et al. 2009). Despite the importance of functional traits, there is still very little information available on functional traits for animal species compared to advancements in plant functional ecology (Cornelissen et al. 2003, Kattge et al. 2011).

The availability of bird trait data is somewhat limited. Information on bird traits are available through literature reviews and measurement of museum specimens, although the latter requires access to quality collections holding enough specimens to obtain mean trait values. Collection of functional traits is extremely valuable as this information can be used to understand ecosystem services delivery at broader scales (Abelleira et al. 2016) complementing rather than competing with current biodiversity monitoring efforts (Vandewalle et al. 2010). Because much of these data are not available for multiple tropical species, mist-netting data may be a valuable source of information in tropical systems.

Trends of population declines for several Neotropical migratory bird species (DeSante et al. 1995) prompted the creation of the Monitoring Overwintering Survival (MoSI) Program whose goal is to collect information about Neotropical migratory bird species in their wintering grounds (DeSante et al. 2005, Saracco et al. 2009). Increases in numbers of locally run mist-netting stations were the result of the creation and establishment of the MoSI Program, which is the Latin American and Caribbean counterpart to the Monitoring Avian Productivity and Survivorship Program (MAPS) run in the United States by the Institute for Bird Populations (IBP) since 1989 (DeSante 1992, Albert et al. 2016). Many of the stations originally established by the MoSI Program are no longer functional as a result of multiple limiting factors and challenges associated with the sustainability of long-term monitoring programs. However, a few of the original MoSI stations continue to collect information following original protocols or variants. Several stations have extended their efforts to collect data related to resident species, filling an important knowledge gap on the basic ecology of tropical birds (Sodhi et al. 2011).

The long-term bird monitoring program at the Tropical Agricultural Research and Higher Education Center (CATIE) is one of the longest running mist-netting stations in Costa Rica, having been established in January 2008 and continuing into the present time. CATIE's bird monitoring program is one of several mist-netting stations in Costa Rica following variations of the MoSI Program protocol. The Landbird Monitoring Program at Tortuguero, established in 1994, is the oldest mist-netting program in the country. However, contrary to the majority of Costa Rican mist-netting efforts, CATIE focuses its efforts in monitoring avian populations within both the agricultural and natural land uses that predominate the Volcanica Central Talamanca Biological Corridor (VCTBC). Long-term monitoring of avian

populations within agricultural land uses is of utmost importance, as 38% of the global ice-free land surface is currently dedicated to crop and pasture lands (Foley et al. 2011) making learning about how avian populations use and persist in human dominated landscapes imperative (Gardner et al. 2009). Additionally, long-term monitoring of avian populations in landscapes with different agricultural land uses will provide a better understanding of potential contributions of agricultural land uses and management practices to forest bird conservation (Harvey et al. 2005, Vílchez-Mendoza et al. 2014, Sekercioglu et al. 2015).

Our goal has been to collect data on avian communities in eight different land uses following a management intensity gradient from forests to sugar cane plantations over a seven year time period. We present results from this sampling effort related to: (1) diversity indices, (2) age and sex distribution, (3) recapture rates, (4) captures of forest dependent species in agricultural land uses, and (5) bird functional traits collected during our sampling efforts. We will discuss the lessons learned from seven years of mist-netting as well as about the challenges of maintaining long-term monitoring programs.

Methods

Study Area

The study was conducted in the Turrialba region of Costa Rica, Central America, primarily on the Tropical Agricultural Research and Higher Education Center (CATIE) main campus and commercial farm. The CATIE property has an area of 1036 ha (lat 9°53’ N, long 83°43’ W) and encompasses a diversity of productive systems. The predominant land uses include forest, cattle pastures, sugar cane and coffee. CATIE is situated within the Caribbean watershed of Costa Rica at 600 m.a.s.l. and corresponds to the very humid pre-montane forest

ecological zone. The average rainfall is 2636 mm, with mean temperature of 22°C and a relative humidity of 87% (CATIE meteorological station *unpublished data*). Rainfall is almost evenly distributed throughout the year but usually decreases between February and April. CATIE is one of the largest farms in the Turrialba valley combining different production activities such as pastures, sugar cane, coffee (*Coffea arabica* var. caturra), forests plantations and reforestation plots, nurseries and small organic agriculture plots. Additionally, the farm also includes approximately 200 ha of secondary forest and a botanical garden where several varieties of coffee, cacao, palms and other tropical species are kept.

CATIE is located at the heart of the 114,626 ha Volcanica Central Talamanca Biological Corridor (VCTBC). Over 50% of the corridor is covered by forests with more than 30% of the remaining area covered by agriculture. Pastures (25%), coffee (9%), shrublands (6%), and sugar cane (4%) being the most important land uses following forest. The VCTBC is a national conservation strategy established in 2003 aiming at reconnecting the Volcanica Central and the Talamanca mountain ranges (Canet 2008). The VCTBC is part of the National Biological Corridors Program managed by the Costa Rica National System of Conservation Areas (SINAC).

General description of selected land uses

Data were collected in eight different land uses within the CATIE campus and commercial farm. These land uses included: (1) a well-preserved mature secondary forest; (2) a multi-strata coffee agroforest system associated with poró (*Erythrina poeppigiana*), a leguminous nitrogen-fixing tree and laurel (*Cordia alliodora*); (3) a simplified agroforest coffee exclusively associated with poró; (4) a multi-strata agroforest cacao (*Theobroma*

cacao) system associated with laurel and banana (*Musaceae sp.*); (5) pasture lands surrounded by live fences; (6) sugar cane (*Saccharum officinarum*); (7) a mixed species forest plantation which includes *Vochysia ferruginea*, *Eucalyptus sp*., *Cedrela sp.*; and (8) a teak (*Tectona grandis*) plantation (Fig. 1).

Land use complexity varied from mature secondary forests to simplified monocultures. Our forest site (FORE) corresponds to our reference system and it exhibits a well-developed understory and mid- and upper level canopy (Fig. 1a). FORE most abundant tree species included *Dendropanax aff. gonatopodus* (Araliaceae), *Spondias radlkoferi* (Anacardiaceae), *Turpinia occidentalis* (Staphyleaceae), *Allophylus psilospermus* (Sapindaceae), *Lonchocarpus guatemalensis* (Fabaceae), *Terminalia oblonga* (Combretaceae) and *Hasseltia floribunda* (Salicaceae). Our two coffee sites differed in vertical structure complexity as one of them is in exclusive association with poró trees (SICO) representing the typical coffee system found in Costa Rica in which arrangement of plots correspond to coffee plants interspersed by poró trees whose branches are radically and regularly (usually twice a year) pruned (Fig. 1d). Poró is a very fast growing leguminous fixing tree, which allows for highly plastic canopy closure. The second coffee site, corresponds to an abandoned multi-strata coffee agroforest plantation (MACO) (Fig. 1c). MACO was abandoned nearly 20 years ago, though its shrub strata is still dominated by coffee plants. It exhibits a well-defined middle strata consisting primarily of formerly pruned poró trees that now reach heights of about 12 m, and an upper strata dominated by laurel trees that can reach 20 m in height. The plot vegetation structure is equivalent to coffee sites managed for Smithsonian Bird Friendly standards which promote avian habitat conservation in coffee (DeClerck and Martínez-Salinas 2011). The multi-strata agroforest cacao land use (MACA) has a vegetation structure similar

to MACO, but in this case cacao shrubs (2-3 m) dominate the understory, interspersed with banana plants and tree canopy height varies from 10 to 25 m (Fig. 1b). Our live fence (LIFE) land use consists of a 300 m long linear row of trees dominated by *Inga* spp. and two species of poró (*E. poeppigiana* and *E. fusca*) (Fig. 1g). These trees form the boundary between pastures with live trees serving as fence posts to which barbed wire is affixed. Networks of fences can serve both as habitat and corridors for birds (Harvey et al. 2005). Pastures are dominated by Tanner grass (*Brachiaria radicans*) with management varying from regularly grazing to fallows of six months or less (particularly in 2010). The two independent forest plantations consist of a mixed species (MSPL) (Fig. 1f) planted in 2008 and a pure teak plantation (TEPL) (Fig. 1e) planted in 2010 (replacing a portion of the MACO site). The system with the simplest vertical structure is sugar cane (SUCA). During sugar cane's production cycle, the plant can reach heights of 2.5 to 3 m, with approximately 1 m spacing between rows. The cane is burnt and harvested once a year, usually in May.

Sampling protocols

We present data from permanent mist-netting stations. Stations were first established in January 2008 in all land use types except MSPL and TEPL, which were established in 2011. Originally, a total of ten mistnets were placed in each land use type, following standard protocols (Ralph et al. 1993). Distance between nets varied between 5-20 m depending on land use. Mistnets have standard dimensions (12 m long x 2.5 m height x 30 mm mesh size) recommended for passerine birds (Ralph et al. 1993). Operation of stations started at 0500 until 0900 with net checks every 40 minutes. Opening and closing times varied by ± 30 minutes depending on weather conditions and season, all variations pertaining to sampling

effort were recorded. During each net round captured birds were removed from nets and placed into individual cloth bags to reduce stress due to handling. They were then carried back to processing stations. All captured birds except hummingbirds and large species for which we did not have appropriate band sizes, were banded using numbered aluminum bands. Resident birds were fitted with Costa Rican Ornithological Association (AOCR) bands following Costa Rican government regulations (Costa Rica Scientific Passport #04541, University of Idaho ACUC protocol #2012-20). Migratory birds were fitted with US Geological Survey (USGS) bands provided under the Institute for Bird Populations (IBP) master bander permit following North American Banding Council (NABC) regulations.

Several variables were evaluated on captured birds including age and sex. Bird's age and sex were defined following protocols described by Ralph et al. (1993) and Pyle (1997). Age classification was determined using a combination of parameters which included skull pneumatization condition and plumage patterns whenever possible. We followed Pyle (1997) age terminology and thus a hatch-year (HY) bird is an individual on its first calendar year (includes the period between fledging until December 31st of the same year), a second-year (SY) bird is an individual in its second calendar year (includes the period between January 1st to December 31st of the year following fledging) and an after hatching-year (AHY) bird is an individual after its first calendar year. It is important to note that the AHY category is very broad and it may include individuals on their second calendar year as accurate age classification of Neotropical birds is extremely difficult due to a tremendous lack of information on molt patterns of most families and species (Pyle et al. 2004, Ryder and Wolfe 2009). Sex classification was determine by color plumage differences in species known to have sexual dimorphism and by presence of cloacal protuberances and brood patches in

species with no differences in plumage coloration (Ralph et al. 1993, Pyle 1997). Cloacal protuberances and brood patches are characteristics of breeding individuals (Pyle 1997) and so the use of these parameters is restricted to the breeding season.

Measurement of bird traits was conducted following protocols described by Ralph et al. (1993) and Pyle (1997). Bird traits measured include: (1) bill length, (2) bill height, (3) bill width, (4) tarsus length, (5) wing length, (6) tail length and (7) weight.

Analyses

We calculated species-accumulation curves (sample-based method) and diversity indices with the *vegan* R package (version 3.1.2) by using the implemented interface in *InfoStat* (Di Rienzo et al. version 2015). Additionally, we used Linear Mixed Models (LMMs) (Zuur *et al.* 2009) to explore differences among land use types for the response variables (i) species richness, (ii) Evenness index, (iii) Shannon index and (iv) Simpson index. Land uses were assigned as fixed effects. For the response variables Shannon and Simpson Index we modeled variance heterogeneity by including a function of specific variances for each land use (R function varIdent). Parameters were estimated via Restricted Maximum Likelihood (REML). Adequacy of models checked graphically via diagnostic graphs. Differences among land uses with respect to response variables were considered to be significant when $P < 0.05$. Comparisons on mean values were evaluated through the *post hoc* LSD Fisher test. Analyses were performed with the *lme4* R package (version 3.1.2) using the implemented interface in *InfoStat* (Di Rienzo et al. version 2015).

Results

General results

From January 2008 through December 2014, a total of 8,750 birds were captured and evaluated as part of our permanent bird monitoring program. Monitoring efforts included 769 sampling dates for a total of 19,446 net hours. The 8,750 individuals captured belong to 205 species distributed amongst 31 families (for a complete list of families and species see Table S1, Chapter 2); 82% of all captured birds were classified as resident species while Neotropical migrants accounted for the remaining 18%. The land use with the highest number of captures was our simplified coffee agroforest (SICO) with over 2,500 individuals (Table 1).

Species richness and Diversity Indices

Our extensive sampling efforts provide valuable information regarding changes in bird community composition (see Chapter 2), abundance, and use along a land use management intensity gradient. We found species richness to be significantly different among sampling units within land use types ($F_{1,7} = 13.29$, $P < 0.0001$) with the SICO land use showing the highest species richness (Fig. 3a). Species richness of land uses at the extremes of the management intensity gradient (FORE and SUCA) are both approaching the asymptote (Fig. 2), suggesting sampling efforts have been sufficient to provide an adequate representation of most species present in these land uses (Gotelli and Colwell 2001, Colwell et al. 2004). However, neither land use have reach a plateau (Fig. 2), also suggesting that after seven years of sampling all land uses might incorporate new species as shown by the mean number of expected species calculated by the Inverse Simpson Index (Table 2).

All diversity indices calculated were significantly different among land uses (Fig. 3 b-d). Evenness ($F_{1,7} = 3.50$, $P = 0.0048$), Shannon-Wiener ($F_{1,7} = 28.54$, $P < 0.0001$), and Simpson ($F_{1,7} = 14.41$, $P < 0.0001$). The MACO land use fosters the most evenly distributed community (Table 2) among land uses. Additionally, the MACO and SICO land uses foster the most species diverse communities also showing the lowest dominance among land uses. Agroforest land uses MACO, SICO and LIFE show the greater number of expected species when compared to other land uses (Fig. 2, Table 2).

Sex and age distribution across land uses

Out of the 8,750 birds captured, we were able to sex 4,998 (57%). A total of 2,515 (29%) were female and 2,483 (28%) male, the remaining individuals (n = 3,752, 43%) were unassigned. Less intensively managed land uses (FORE, MACO, MACA, SICO and MSPL) showed higher proportions of females than males. SICO and MSPL particularly exhibited 3 to 8% more females respectively. In contrast, SUCA, our most intensively managed land use, exhibited the greatest difference in sex distribution with 12% more males than females (Table 3).

We were able to assigned 8,237 (94%) birds to either the hatching year (HY), second year (SY) and after hatching year (AHY) categories (Table 4). The majority of individuals captured across land uses were identified as adults (AHY, 64%) followed by juveniles (HY, 23%) (Fig. 4, Table 4). Across land uses, overall capture rates of resident juvenile (HY) birds peaked during June, July and August (Fig. 4). Resident juveniles during this three month period corresponded to 44% of all resident juvenile birds captured (n = 1761). In addition, numbers of migratory juvenile (HY) birds peaked during the fall migration, particularly

during October (Fig. 4). Migratory juveniles captured in October corresponded to 47% of all migratory juvenile birds captured (n = 252). For details about age distribution for resident and migratory birds per land use see Fig. S1-S8.

Recapture rates

Recapture rates varied depending on land uses and whether individuals were residents or migrants. Overall the majority of individuals captured corresponded to new individuals/first time captures (n = 4,695; 54%), followed by unbanded individuals (n = 2,174; 25%) which correspond to those measured and released without any markings, and recaptures (n = 1,881; 21%) which corresponds to previously captured individuals.

Migratory bird recapture rates differed across land uses. The SICO land use showed the highest intra-season, inter-season and inter-year recapture rates (Table 5). Intra-season recaptures defined as those individuals recaptured during the August-April period (Fig. 5a), inter-season recaptures defined as individuals recaptured either during the spring (January-April) or fall (August-December) migration within the same year (Fig. 5b) and inter-year recaptures defined as individuals recaptured between seasons and years (i.e. Oct.25.2010 – Feb.24.2012, Fig. 5c). Out of the 1,572 migratory individuals captured, 202 (13%) have been recaptured, with 51% recaptures during the intra-season period, 42% recaptures during the inter-year period and 7% recaptures during the inter-season period. Recapture frequencies varied from one to six with 71% of individuals being one time recapture followed by two times recapture (18%), with the remaining 11% distributed among the three to six time recapture frequency categories. Additionally, 90% (n = 181) of individuals recaptures have

occurred within the same land use with only 10% (n = 21) recaptures outside of the original land use were first captured (Table 5).

Resident bird recapture rates differed across land uses. The FORE land use showed the highest resident recapture rate with 31%, followed by TEPL (23%) and SICO (23%). Resident recapture rate was greater than 20% across land uses with the exception of SUCA (16%) and MSPL (12%) (Table 6).

Forest dependent species and agricultural land uses

Through our permanent monitoring efforts we have been able to collect evidence of forest bird species using different agricultural land uses. Here we provide examples of three bird species that according to Stiles (1985) are forest interior and forest edge dependent and need at least patchy forest for their survival. During the years 2008 to 2014 twelve White-ruffed Manakin *Corapipo altera* (Pipridae) individuals have been captured, two of which were banded and recaptured within our FORE land use, one month and two years after their first capture respectively. About half of the individuals of *C. altera* have been captured in our FORE (n = 6, 55%) land use. However, the remaining individuals were captured in agroforesry land uses, including MACO (n = 1), MACA (n = 3), SICO (n = 1) and LIFE (n = 1); and in all but one case, individuals captured were identified as juveniles either in their first year (HY) or second year (SY) of life. A second forest dependent species, Chestnut-backed Antbird *Myrmeciza exsul* (Thamnophilidae), has been captured in MACO on at least five independent occurrences. All but one of the *M. exsul* individuals captured were male, two were juveniles and three adults. Two of the individuals had previously captured in the same land use, one month and four years after their initial capture respectively. Finally, 218 Ochre-

bellied Flycatcher *Mionectes oleagineus* (Tyrannidae) individuals, a small insectivorous bird have been captured mainly in FORE (n = 86, 39%) but also in another six different land uses, MACO (n = 46), MACA (n = 33), SICO (n = 41), MSPL (n = 1), LIFE (n = 9) and SUCA (n = 2). The majority of captures outside of FORE are restricted to agroforestry land uses which together comprise 55% of all new individuals captured. Furthermore, 180 *M. oleaginous individuals* have been recaptured, the highest recapture of any species found in FORE (67%) the remaining recaptures are divided between the agroforestry sites (MACO, MACA and SICO), with no recaptures in our intensively managed land uses (LIFE and SUCA) despite a few captures. Finally, *M. oleagineus* individuals recaptured outside of FORE were primarily juveniles (47%) with the remaining individuals divided between adults (44%) and individuals that were not assigned to any age category (9%).

Functional traits

Information about bird functional traits have been collected for over 100 bird species. Table S3 summarizes mean values plus standard deviation for seven morphological functional traits for tropical resident bird species.

Discussion

Long-term mist-netting is a powerful technique that allows collection of valuable information about avian populations, however needs to be considered carefully within the limitations of the method. Specifically, mist-nets are more effective at capturing individuals moving in lower elevations (Ralph et al. 1993, Dunn and Ralph 2004). Our results are therefore based on communities susceptible to mist-netting protocols and should not be

regarded as a comprehensive representation of communities inhabiting these land uses, particularly those that are more vertically complex such as agroforestry systems and forests. For a complete representation of communities mist-net data should be complemented with observational methods as to incorporate species moving beyond the realm of mist-net effectiveness. Discussion and conclusions drawn from our mist-netting data should therefore be considered within these limitations.

Our results show that agroforestry systems exhibited the highest species richness, the most uniformly distributed communities, the highest species diversity and lowest dominance as well as the greatest number of expected species across land uses. Coffee agroforestry systems whether simplified or multi strata showed the most diverse communities with the lowest dominance and are expected to incorporate the greatest number of new species compared to the remaining land uses. These results highlight the importance of coffee systems for bird conservation as shown by similar studies (Petit and Petit 1999, Petit and Petit 2003). It is important however to consider that conservation value of these systems is dependent on management interventions and such should be aimed at maintaining or enhancing characteristics that fosters biodiversity conservation (Greenberg et al. 1997a).

Agroforestry systems such as life fences revealed fostering diverse bird communities. Our LIFE land use follow coffee systems in all metrics except evenness where the TEPL site showed a more evenly distributed community following the MACO system. Life fences which are predominant structures in many Central American agricultural landscapes (Harvey et al. 2005) exhibited high conservation value when compared to other less intensively managed land uses. Live fences play important roles at providing habitat and food resources (Harvey et al. 2005, Sánchez et al. 2005, Chacón and Harvey 2006, Vilchez-Mendoza et al.

2014). However, as pasture lands cover on average one quarter of the territory of Central American countries, with 45.8% of the Costa Rican territory occupied by these land use (The Nature Conservancy 2005) more information is needed regarding the use of these elements as connectors between habitat patches as well as to their contribution at facilitating species movement and ecosystem services delivery (Fremier et al. 2013) within agricultural landscapes.

Based on individuals that were successfully assigned to a sex category, our results show higher proportions of females in less intensively managed land uses such as forests and agroforestry systems. We could argue the emergence of sexual segregation depending on habitat quality, as less intensively managed land uses might be providing with better habitat and food resources (Reitsma et al. 2001, Luck and Daily 2003, Van Bael et al. 2007). However, these results should be considered carefully as 43% of individuals captured were not assigned to either sex category and so further sex assignment might reverse this trend. Additional information about changes in food resource availability and vegetation structure within each of our monitored land uses will be necessary to explore causes of this potential sexual segregation (Parrish and Sherry 1994, Morales et al. 2008). Particularly as several studies show opposite trends with male individuals occupying higher quality habitats (Lopez Ornat and Greenberg 1990, Parrish and Sherry 1994, Mettke-Hofmann et al. 2015).

Age structure across our land uses shows an almost even distribution between adults and juvenile birds. Our long-term mist-netting efforts have allowed us to learn about annual temporal changes in mean abundance of adults and juveniles (Fig. 4, Fig. S1-S8). Identification of these temporal changes is particularly important for resident bird species as to provide with information about prime timing for management interventions within these

habitats. Management interventions such as shade pruning (Beer et al. 1998) which is a common practice within our SICO land use and across coffee plantations in Central America (Haggar et al. 2011), might have detrimental effects on bird populations and should if possible be conducted outside of sensitive periods such as the breeding season.

Recapture rates which is an important indication of site fidelity varied across sampling units within land uses and depending on residency status. Our results show resident species recapture rates to be the highest (31%) within our FORE land use. The FORE land use is characterized for fostering a unique bird community (see Chapter 2) with low diversity and high dominance of species when compared to the remaining land uses (Table 2). FORE resident recapture rates suggests high site fidelity, similar to Kricher and Davis' (1998) findings where recapture rates were higher in young and mature forests compared to abandoned agriculture fields. Migratory bird species recapture rates on the other hand, were the highest within the SICO land use whether considering intra-season, inter-season or inter-year recaptures. The greater number of recaptures occurred during the intra-season which is an indication of individuals overwintering within these land uses (Petit et al. 1995), providing additional evidence of the importance of managing these systems for Neotropical migratory species conservation (Perfecto et al. 1996, Petit et al. 1999). Studies highlighting habitat use by migratory species are particularly important to understand the ecology of resident communities (Latta and Faaborg 2008). Additionally, information about capture and subsequent recapture of either resident or migratory bird species is needed to build capture-recapture histories for estimating apparent survival probabilities (DeSante et al. 1995). Apparent survival probability is an important characteristic of wild populations; however there are few studies that have produce these probability estimates for tropical bird species

(but see Wilson et al. 2011, Ruiz-Gutierrez et al. 2012, Mumme et al. 2015, Saracco et al. 2016) due to difficulties involving maintenance of long-term mist-netting efforts which provide data for robust estimations. Our long-term monitoring efforts are aiming at producing such estimates and thus contribute to narrow this knowledge gap.

Effective dispersal events of individuals are critical in the maintenance of spatial dynamics of bird populations persisting in agricultural land uses. Recapture of individuals between several of our sites provides evidence that forest dependent species are using agricultural land uses during dispersal events. White ruffed-Manakin, Chestnut-backed Antbird and Ochre-bellied Flycatcher individuals have been captured in all monitored agricultural sites with higher proportion of captures in agroforestry systems including live fences. The majority of individuals captured were identified as juveniles suggesting the use of alternative land uses during dispersal events and highlighting the importance of the matrix composition and configuration (Estrada-Carmona et al. In Review) in enabling these types of movements (Vandermeer and Carvajal 2001) and thus maintaining functional connectivity (Martensen et al. 2008) within agricultural landscapes. Despite the importance of dispersal events in the maintenance of metapopulations (Levins 1969) very little information is known about dispersal capabilities of tropical bird species (but see Moore et al. 2008) particularly regarding the impact of vegetation structures that birds may or may not utilize during dispersal events (but see Castellon and Sieving 2006). As mentioned before live fences for example, are predominant elements in most Central American landscapes (Harvey et al. 2005) however more information is needed to accurately assess their role in facilitating dispersal movements of forest dependent species (Estrada-Carmona et al. In Review). We have captured forest dependent birds dispersing through these linear elements, however we are

missing information to determine whether these dispersal events contribute to meta-population growth and stability.

Collection and publication of functional trait measurements is important to advance studies in functional ecology. Collection of morphological traits of highly mobile organisms is extremely difficult, compelling researchers to use functional traits available through existing literature (Flynn et al. 2009, Philpott et al. 2009, Newbold et al. 2012, Luck et al. 2013, Barbaro et al. 2014) or through measurement of specimens from museum collections. Mist-netting stations have the unique opportunity to collect this information on a regular basis and thus we encourage mist-netting managers to add the collection of morphological traits to their sampling protocols. As part of our monitoring efforts we have provided here mean values ± SD for seven morphological traits from over 100 resident bird species from Central America (Table S1).

Establishment and long-term operation of mist-netting stations is not an easy task. There are no doubts that mist-netting stations have the capacity of generating vast amounts of information about avian populations (Sekercioglu 2012). However establishment and long-term operation is challenging as it requires qualify technical personnel to run stations safely and steady funds that allow payment of personnel along with replacement of damaged equipment. During our years of operation we have managed to obtain funds through different funding sources however despite the importance of mistnetting operations (Dunn and Ralph 2004), availability of funding opportunities for long-term monitoring are becoming harder to procure which may jeopardize the future of our stations as well as other similar efforts. Given the dynamic nature of landscapes conversion in the tropics (Laurance and Bierregaard 1997), it remains important to have mist-netting stations in land uses different than forests,

particularly in agricultural land uses (Daily et al. 2001) which depending on management might provide with habitat and dispersal pathways (Sekercioglu et al. 2015) for species of conservation concern.

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Tables

Table 1. Absolute species richness (S) and abundance (Abu) per land use for the years 2008 to 2014 for secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), and sugar cane (SUCA); and for the years 2011 to 2014 for teak plantation (TEPL) and mixed species plantation (MSPL). For details about migratory and resident abundances and net effort per land use see Table 1, Chapter 2.

Land use	2008		2009		2010		2011		2012		2013		2014		Total	
	S	Abu	S	Abu	S	Abu	S	Abu	S	Abu	S	Abu	S	Abu	S	Abu
FORE	26	129	21	56	19	81	24	98	23	118	21	63	19	73	51	618
MACO	64	423	62	236	45	166	35	124	29	70	28	61	23	81	105	1161
MACA	46	219	44	194	60	233	42	156	51	174	31	99	28	115	102	1190
SICO	51	355	52	284	63	445	60	588	61	495	46	202	43	206	118	2575
TEPL							2	2	13	36	9	38	21	86	32	162
MSPL							11	29	35	140	21	62	18	68	50	299
LIFE	50	277	42	173	54	308	50	260	54	356	39	156	35	174	93	1704
SUCA	37	215	19	101	28	166	28	174	35	219	19	77	23	89	60	1041
Total	126	1618	115	1044	125	1399	118	1431	123	1608	103	758	95	892	205	8750

Table 2. Mean values ± standard deviation of Species Richness (S), Evenness (J'), Shannon-Wiener (H'), Exponential Shannon-Wiener (Exp. H'), Simpson (λ), 1-Simpson (1- λ) and the Inverse of Simpson (1/ λ) indices, where secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), sugar cane (SUCA), teak plantation (TEPL) and mixed species plantation (MSPL).

Land use	S	J'	H'	Exp. H'*	λ	1 - λ*	1/ λ*
FORE	21.86 ± 2.61	0.74 ± 0.07	2.29 ± 0.20	10.03 ± 1.96	0.82 ± 0.04	0.18 ± 0.04	5.96 ± 1.43
MACO	41.00 ± 16.57	0.86 ± 0.05	3.13 ± 0.27	23.66 ± 6.06	0.93 ± 0.02	0.07 ± 0.02	15.24 ± 3.65
MACA	43.14 ± 11.05	0.79 ± 0.05	2.94 ± 0.32	19.82 ± 6.54	0.88 ± 0.05	0.12 ± 0.05	9.69 ± 3.78
SICO	53.71 ± 7.78	0.79 ± 0.02	3.16 ± 0.09	23.62 ± 2.10	0.93 ± 0.01	0.07 ± 0.01	13.37 ± 1.81
LIFE	46.29 ± 7.59	0.81 ± 0.04	3.09 ± 0.20	22.34 ± 4.02	0.92 ± 0.03	0.08 ± 0.03	13.09 ± 3.64
SUCA	27.00 ± 7.19	0.76 ± 0.05	2.47 ± 0.20	12.08 ± 2.71	0.86 ± 0.03	0.14 ± 0.03	7.37 ± 1.66
TEPL	11.25 ± 7.93	0.84 ± 0.10	1.71 ± 0.72	6.49 ± 3.57	0.73 ± 0.16	0.27 ± 0.16	4.53 ± 2.13
MSPL	21.50 ± 9.98	0.77 ± 0.05	2.28 ± 0.27	10.02 ± 2.36	0.82 ± 0.05	0.18 ± 0.05	5.65 ± 1.31

*Exponential Shannon-Wiener (Exp. H'**)**, 1 – Simpson (1 - λ) and inverse of Simpson (1/ λ**)** included to facilitate interpretation of indices values.

Table 3. Sex distribution per land use for the years 2008 to 2014 for secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), and sugar cane (SUCA); and for the years 2011 to 2014 for teak plantation (TEPL) and mixed species plantation (MSPL). F = female, M = male, U = undetermined.

Land use	Sex	Abu	%	Proportion	Land use	Sex	Abu	%	Proportion
FORE	F	90	14.56	0.15	TEPL	F	47	29.01	0.29
	M	62	10.03	0.10		M	54	33.33	0.33
	U	466	75.41	0.75		U	61	37.65	0.38
MACO	F	333	28.68	0.29	MSPL	F	113	37.79	0.38
	M	254	21.88	0.22		M	90	30.10	0.30
	U	574	49.44	0.49		U	96	32.11	0.32
MACA	F	349	29.33	0.29	LIFE	F	496	29.11	0.29
	M	272	22.86	0.23		M	626	36.74	0.37
	U	569	47.82	0.48		U	582	34.15	0.34
SICO	F	810	31.46	0.31	SUCA	F	277	26.61	0.27
	M	719	27.92	0.28		M	406	39.00	0.39
	U	1046	40.62	0.41		U	358	34.39	0.34

Table 4. Age distribution per land use for the years 2008 to 2014 for secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), and sugar cane (SUCA); and for the years 2011 to 2014 for teak plantation (TEPL) and mixed species plantation (MSPL). HY = hatching year, SY = second year, AHY = after hatching year and U = undetermined.

Land use	HY	%HY	SY	%SY	AHY	%AHY	U	%U	Total
FORE	151	24.43	75	12.14	350	56.63	42	6.80	618
MACO	216	18.60	128	11.02	740	63.74	77	6.63	1161
MACA	251	21.09	65	5.46	788	66.22	86	7.23	1190
SICO	569	22.10	187	7.26	1663	64.58	156	6.06	2575
LIFE	391	22.95	91	5.34	1144	67.14	78	4.58	1704
SUCA	330	31.70	62	5.96	600	57.64	49	4.71	1041
MSPL	63	21.07	11	3.68	207	69.23	18	6.02	299
TEPL	48	29.63	8	4.94	99	61.11	7	4.32	162

Table 5. Intra-season, inter-season and inter-year migratory recaptures where secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), sugar cane (SUCA), teak plantation (TEPL) and mixed species plantation (MSPL). Where two land uses are present indicates capture and recaptures occurred in different land uses.

Land use	Intra-season	Inter-season	Inter-year	Total
FORE	1			1
MACO	13	3	12	28
MACA	13	2	9	24
SICO	48	8	36	92
LIFE	13	1	11	25
SUCA	6		3	9
MSPL			1	1
TEPL			1	1
MACO-SUCA			1	1
MACO-MACA	3		5	8
SUCA-SICO	1			1
SUCA-LIFE	1			1
MACA-MACO	3		1	4
MACA-SICO		1	3	4
SICO-MACA			1	1
LIFE-SICO			1	1
Total	102	15	85	202

Table 6. Total number of new banded (N), recaptures (R) and unbanded (U) Resident birds across land uses. Years 2008 to 2014 for secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), and sugar cane (SUCA); and years 2011 to 2014 for teak plantation (TEPL) and mixed species plantation (MSPL).

Land use	Resident						
	N	%N	R	%R	U	%U	Total R
FORE	188	31.18	189	31.34	226	37.48	603
MACO	395	41.49	209	21.95	348	36.55	952
MACA	279	29.40	197	20.76	473	49.84	949
SICO	889	47.41	437	23.31	549	29.28	1875
TEPL	66	45.52	34	23.45	45	31.03	145
MSPL	99	40.41	29	11.84	117	47.76	245
LIFE	908	61.43	317	21.45	253	17.12	1478
SUCA	644	69.17	153	16.43	134	14.39	931
Total	3468	48.31	1565	21.80	2145	29.88	7178

Figures

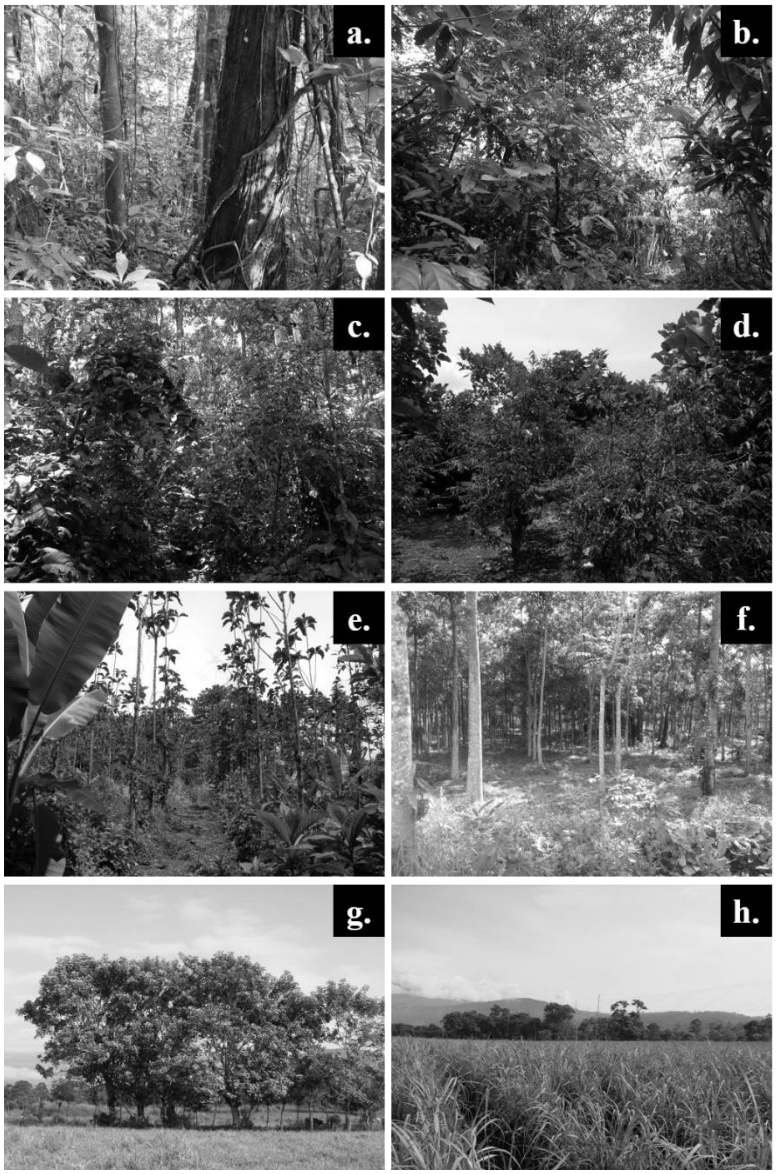

Figure 1. Different land use types included in the CATIE monitoring effort: (a) secondary mature forest (FORE), (b) multi-strata cacao agroforest (MACA), (c) multi-strata coffee agroforest (MACO), (d) simplified coffee agroforest (SICO), (e) teak plantation (TEPL), (f) mixed-species plantation (MSPL), (g) pastures with live fences (LIFE), and (h) sugar cane (SUCA).

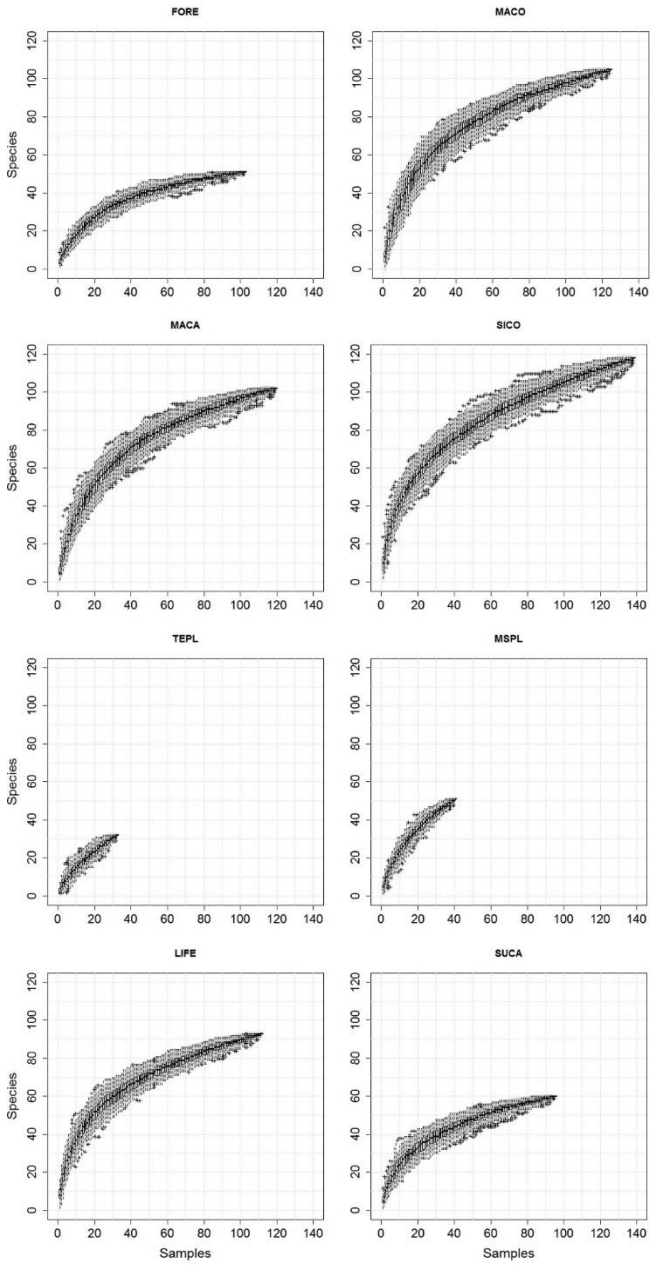

Figure 2. Species accumulation curves (sample-based method) for birds captured in each land use: secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), sugar cane (SUCA), teak plantation (TEPL) and mixed species plantation (MSPL). The Y axis shows bird species and the X axis shows number of samples taken on each land use over the course of seven years for each land use. TEPL and MSPL samples are for 2010-2012 only.

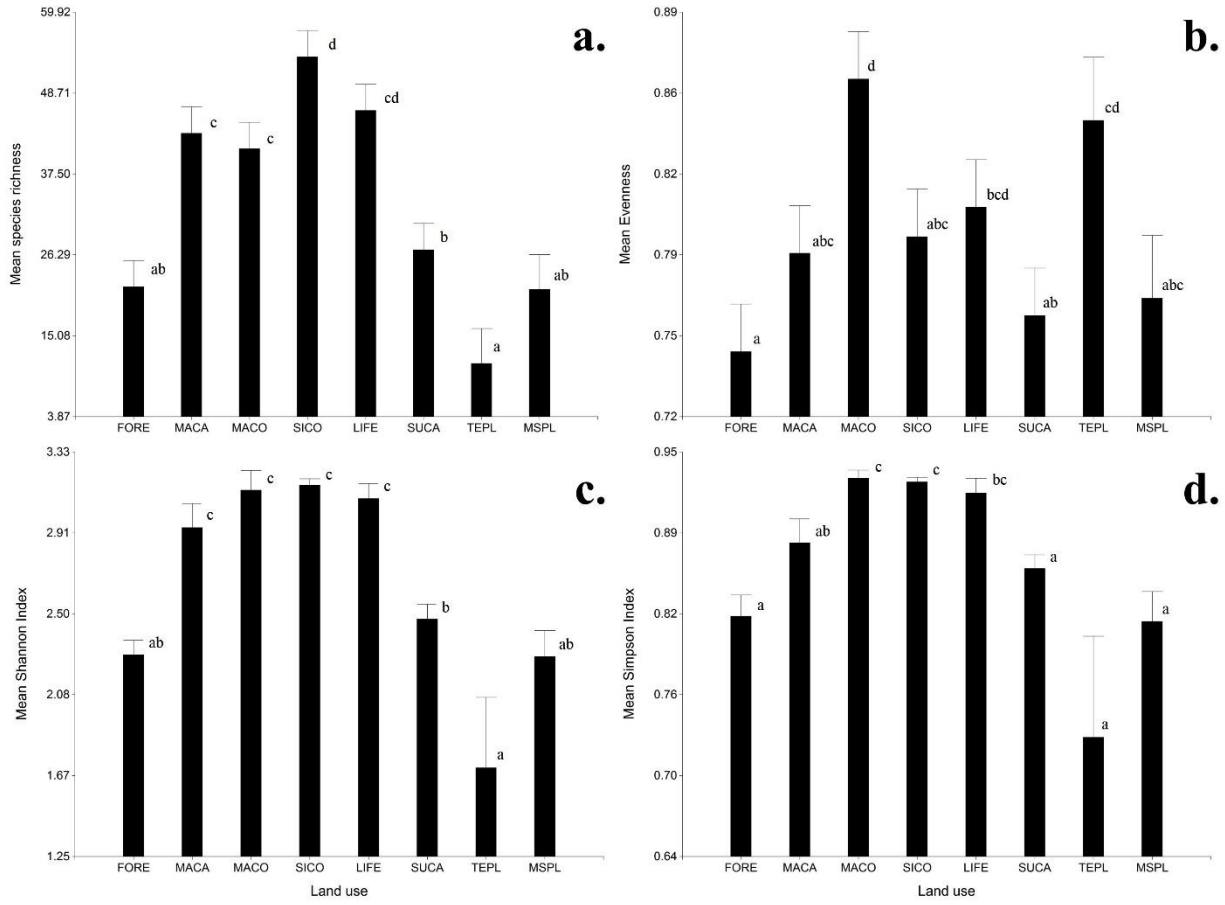

Figure 3. Differences in mean (a) species richness, (b) evenness, (c) Shannon Index, and (d) Simpson Index across sampling units within land use types. Different letters indicate significant differences $P < 0.05$. Bars in graphs show mean values and standard errors where secondary mature forest (FORE), multi strata cacao agroforest (MACA), multi strata coffee agroforest (MACO), simplified coffee agroforest (SICO), live fences (LIFE), sugar cane (SUCA), teak plantation (TEPL) and mixed species plantation (MSPL).

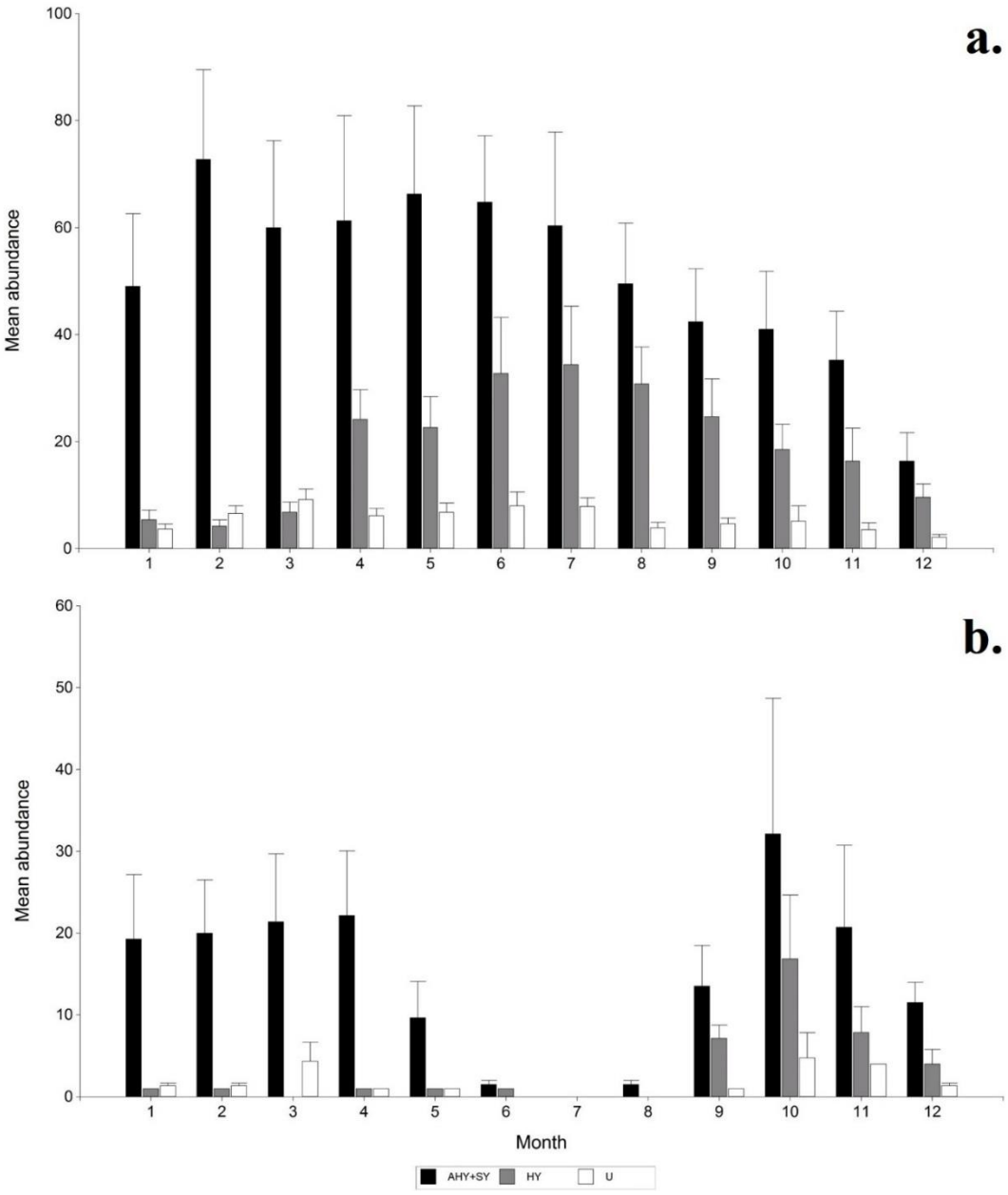

Figure 4. Mean seasonal abundance of (a) resident and (b) migratory birds across land uses (2008 to 2014). Bars in graphs show mean values and standard errors. AHY+SY = after hatching year + second year, HY = hatching year, U = undetermined.

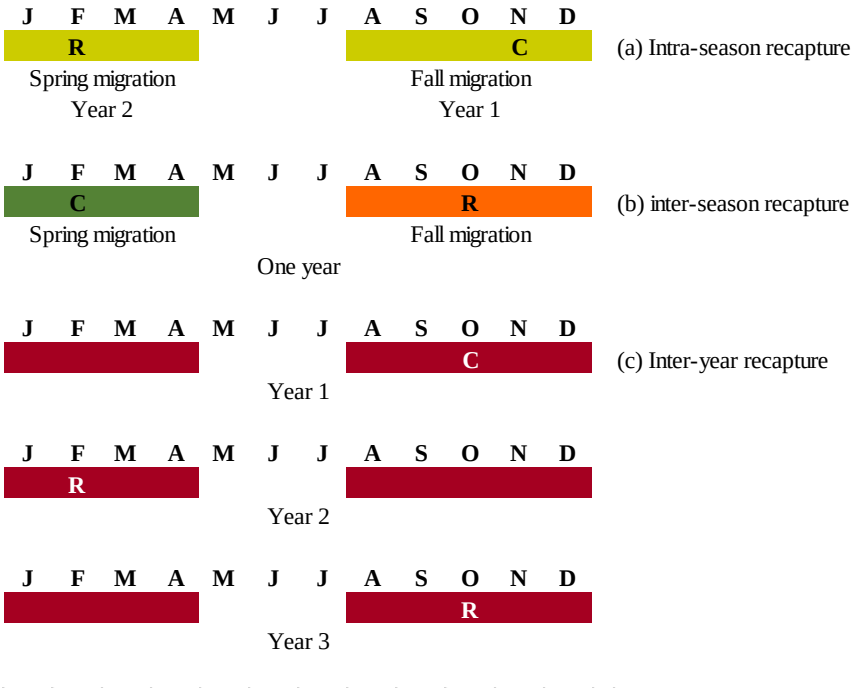

Figure 5. Diagram of time periods considered for intra-season, inter-season and inter-year recapture categories.

Supplementary Information

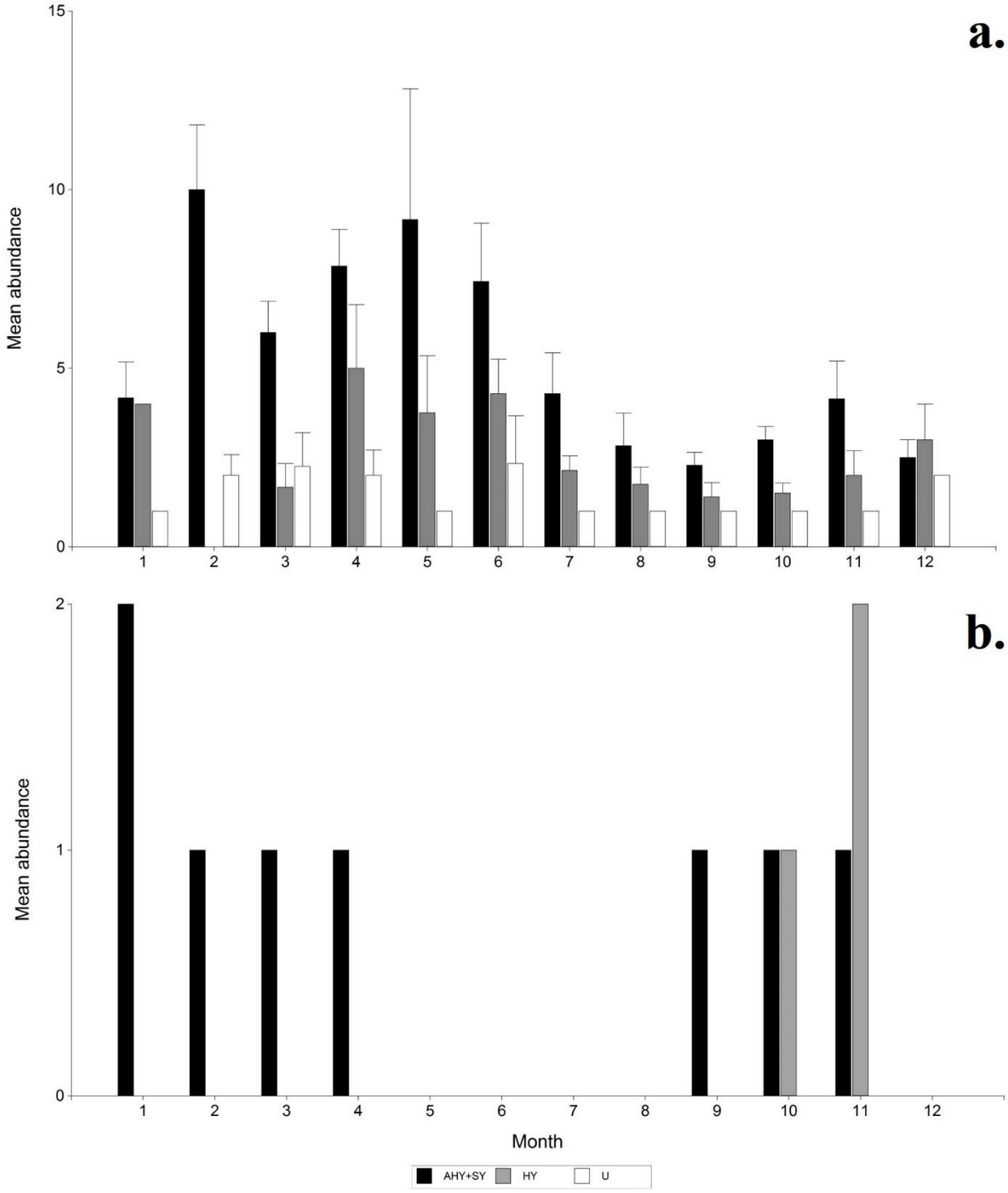

Figure S1. Mean abundance of (a) resident and (b) migratory birds in our secondary mature forest (FORE) land use for the years 2008 to 2014. Bars show standard errors.

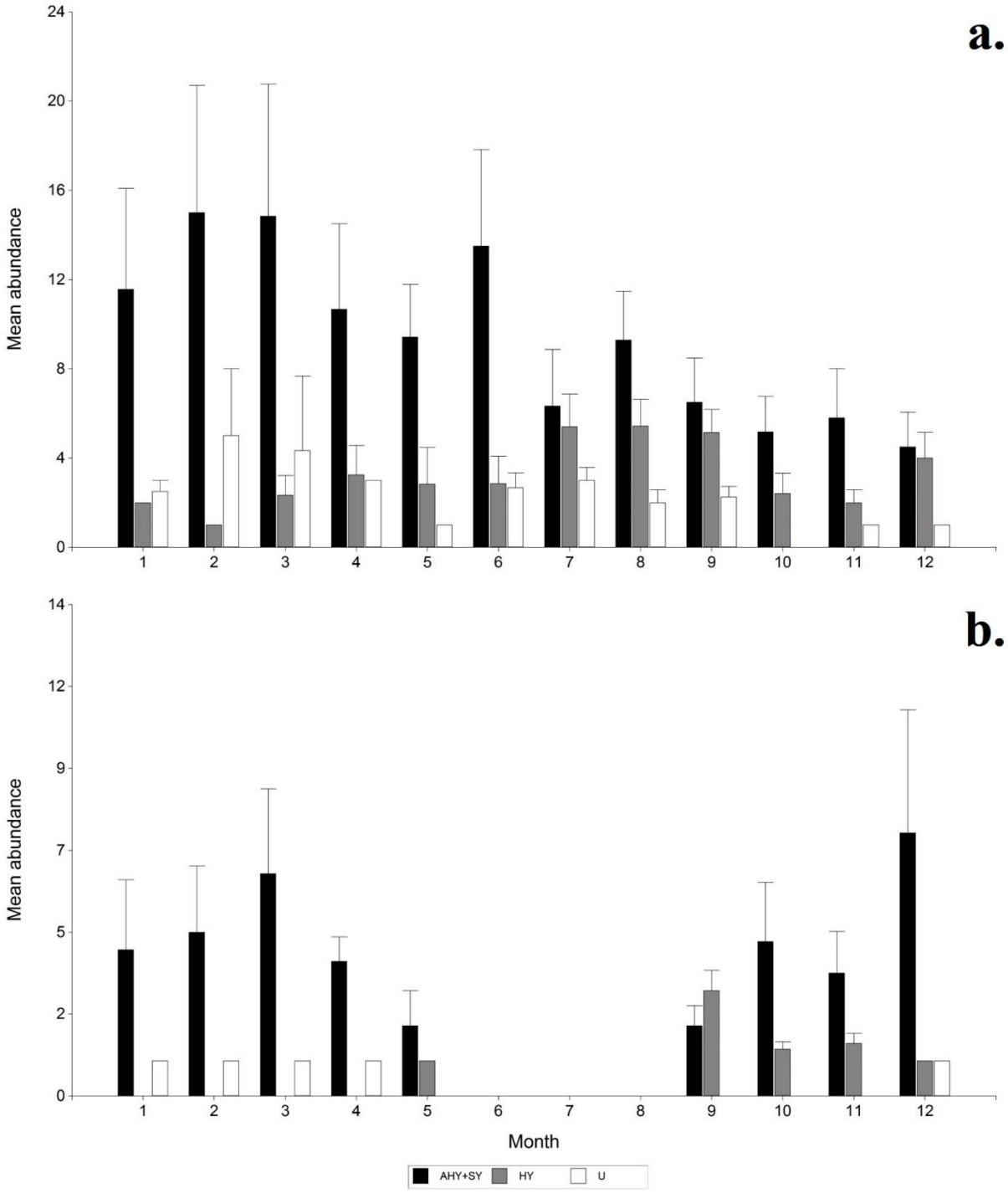

Figure S2. Mean abundance of (a) resident and (b) migratory birds in our multi strata coffee agroforest (MACO) land use for the years 2008 to 2014. Bars show standard errors.

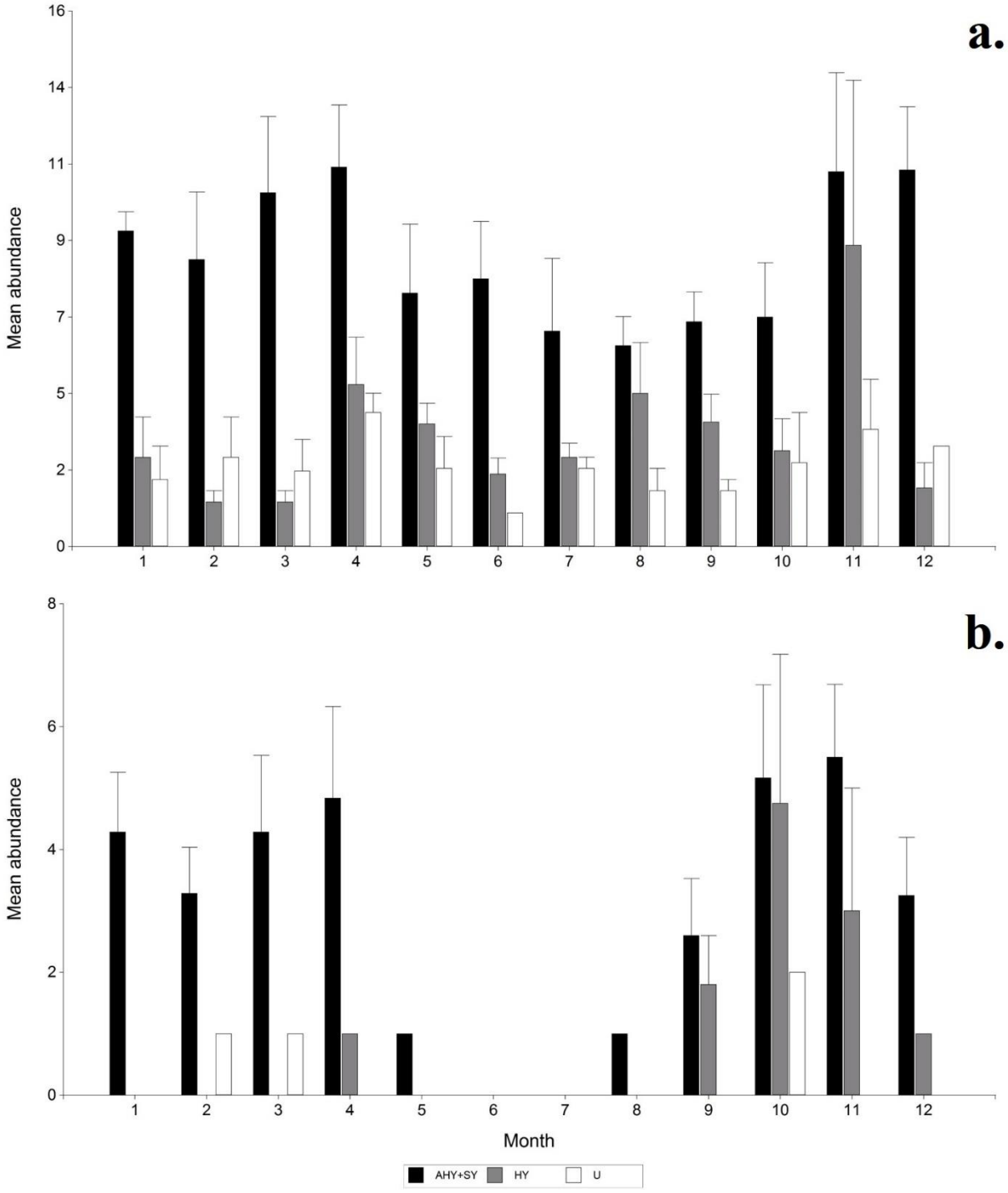

Figure S3. Mean abundance of (a) resident and (b) migratory birds in our multi strata cacao agroforest (MACA) land use for the years 2008 to 2014. Bars show standard errors.

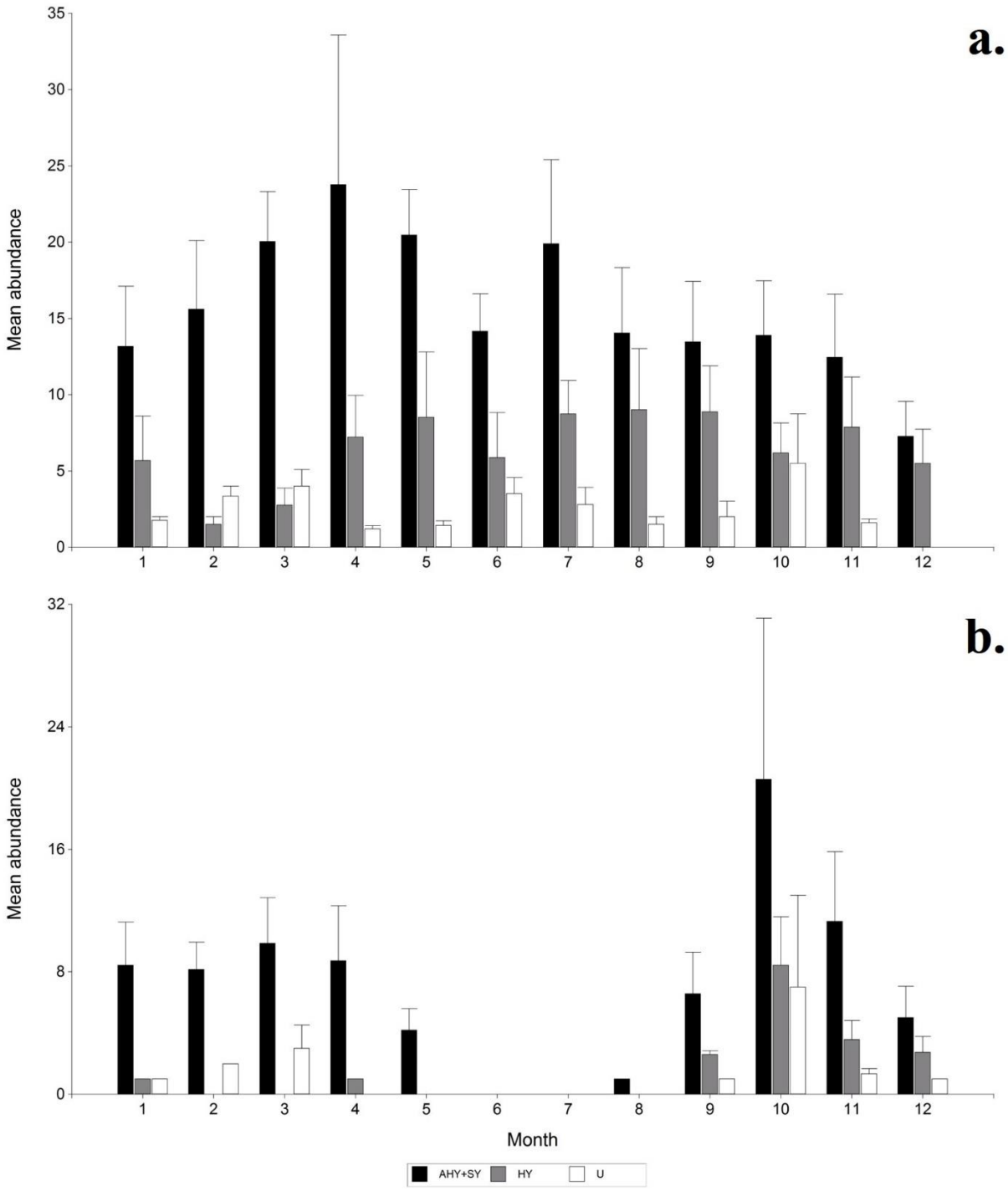

Figure S4. Mean abundance of (a) resident and (b) migratory birds in our simplified coffee agroforest (SICO) land use for the years 2008 to 2014. Bars show standard errors.

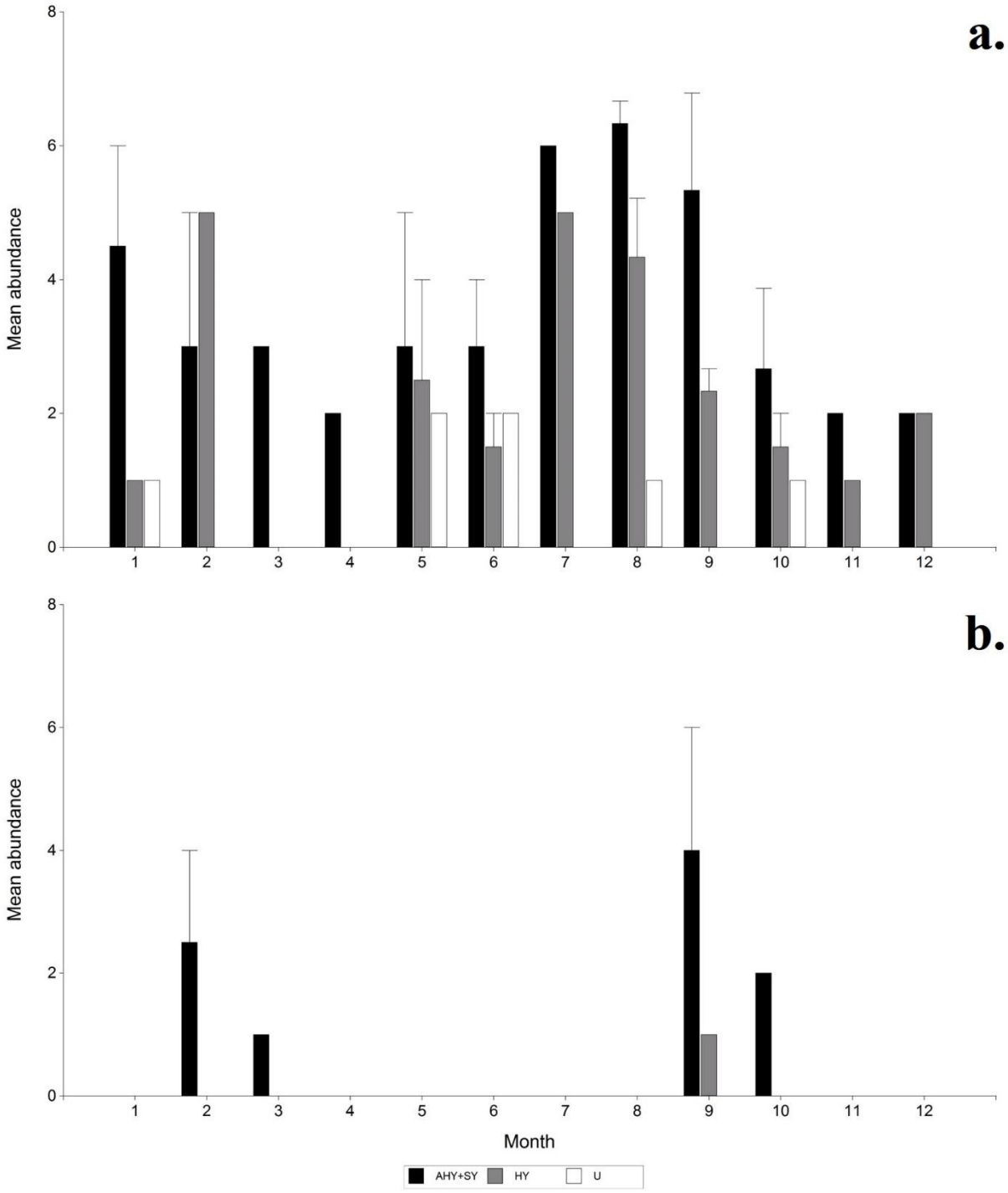

Figure S5. Mean abundance of (a) resident and (b) migratory birds in our teak plantation (TEPL) land use for the years 2011 to 2014. Bars show standard errors.

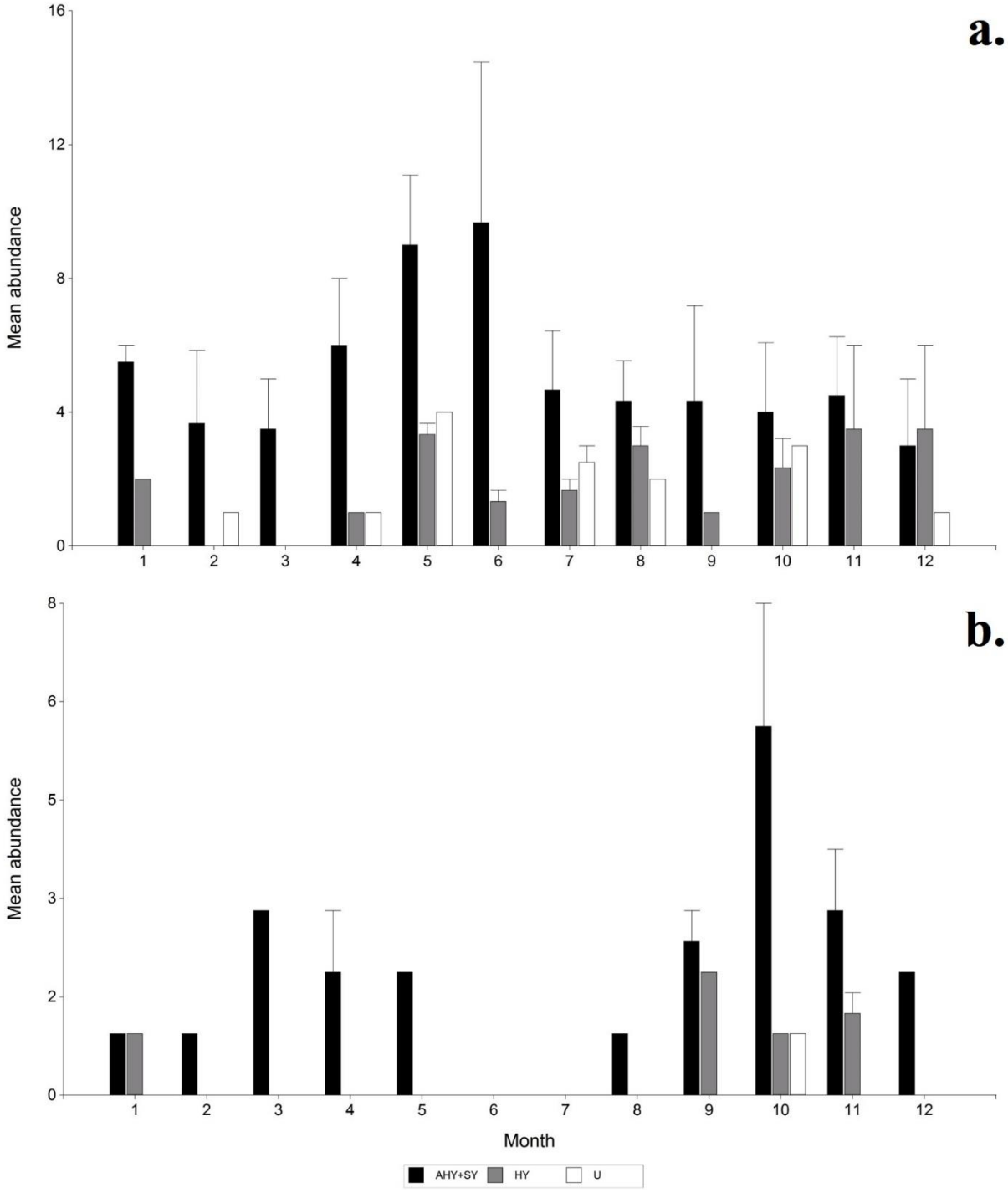

Figure S6. Mean abundance of (a) resident and (b) migratory birds in our mixed species plantation (MSPL) land use for the years 2011 to 2014. Bars show standard errors.

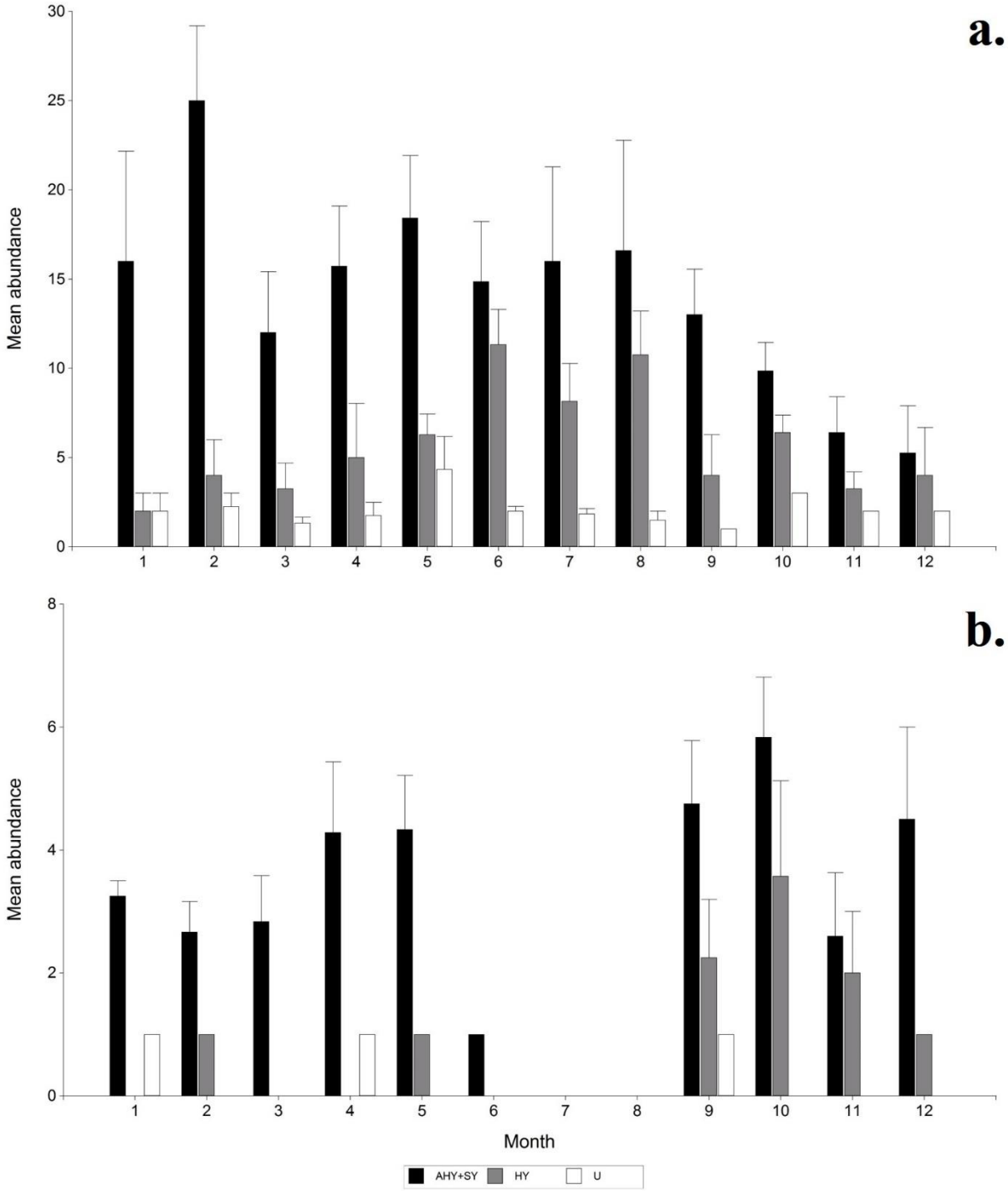

Figure S7. Mean abundance of (a) resident and (b) migratory birds in our life fence (LIFE) land use for the years 2008 to 2014. Bars show standard errors.

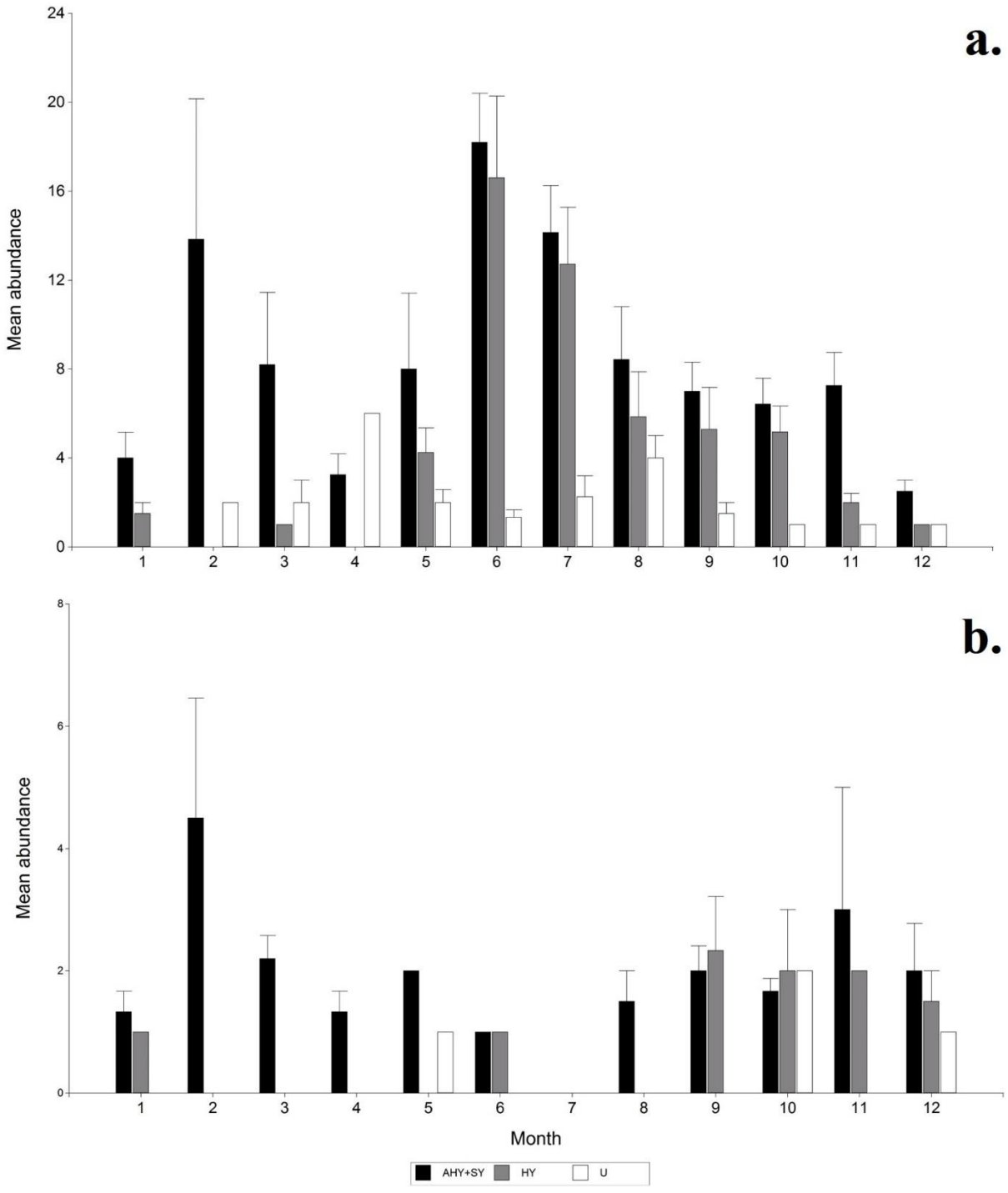

Figure S8. Mean abundance of (a) resident and (b) migratory birds in our sugar cane (SUCA) land use for the years 2008 to 2014. Bars show standard errors.

Table S1. Mean value ± standard deviation of bird functional traits. Values of bill length, bill height, bill width, tarsus, wing length and tail are giving in millimeters (mm), weight values are given in grams (gr). Sample sizes are given in parenthesis. A complete list of English and Latin names is provided in Table S2.

Species Code	Bill length	Bill height	Bill width	Tarsus	Wing	Tail	Weight
AMATZA	21.41(26) ± 2.29	2.31(26) ± 0.49	3.17(26) ± 0.46	5.57(25) ± 1.15	58.47(26) ± 3.00	34.22(9) ± 1.56	5.49(26) ± 0.54
AMBHOL	29.13(1)	10.56(1)	7.43(1)	36.77(1)	99.00(1)	90.00(1)	66.00(1)
ANTPRE	24.74(4) ± 1.27	2.55(4) ± 0.11	3.36(4) ± 0.24	4.48(4) ± 0.74	65.88(4) ± 3.97	36.00(4) ± 1.83	7.25(4) ± 0.50
ARRCON	15.27(2) ± 1.21	8.47(2) ± 0.49	6.07(2) ± 0.02	32.79(2) ± 0.60	73.50(2) ± 2.12	64.00(2)	29.50(2) ± 4.95
ATTSPA	23.49(3) ± 0.78	6.68(3) ± 0.45	7.52(3) ± 0.58	28.38(3) ± 1.87	88.50(3) ± 3.50	71.00(2) ± 4.24	40.00(3) ± 3.00
AUTOCH	22.54(2) ± 0.19	6.73(2) ± 0.01	5.10(2) ± 0.02	28.21(2) ± 0.30	84.00(2) ± 1.41	67.50(2) ± 2.12	41.00(1)
BARMAR	45.00(1)	16.00(1)	13.00(1)	37.00(1)	158.00(1)	276.00(1)	190.00(1)
BASRUF	11.00(2)	4.00(2)	4.00(2)	23.25(2) ± 0.35	56.25(2) ± 1.77		11.50(2) ± 0.71
BUTVIR	62.00(1)	11.09(1)	8.72(1)	54.12(1)	178(1)	64(1)	177(1)
CAMPHEM	31.00(1)	2.50(1)	3.50(1)	6.50(1)	77.00(1)	58.00(1)	8.00(1)
CANMOD	18.16(13) ± 3.42	3.73(13) ± 0.23	3.63(13) ± 0.29	24.69(13) ± 6.71	56.04(13) ± 1.73	49.72(9) ± 2.22	17.77(13) ± 1.42
CANNIG	15.46(7) ± 4.66	3.72(7) ± 1.12	3.49(7) ± 1.02	24.09(7) ± 7.12	65.21(7) ± 6.49	47.38(4) ± 14.48	23.74(7) ± 4.33
CERTYR	20.00(1)	6.50(1)	6.00(1)	26.00(1)	66.00(1)		23.00(1)
COEFLA	13.03(1)	3.39(1)	3.38(1)	19.33(1)	54.00(1)	31.00(1)	9.00(1)
COLTHA	19.12(1)	1.96(1)	2.99(1)	5.01(1)	66.50(1)	40.50(1)	6.00(1)
COLMIN	5.90(1)	1.57(1)	1.69(1)	9.26(1)	85.00(1)	61.00(1)	39.00(1)
COLTAL	12.33(10) ± 0.55	3.31(10) ± 0.23	3.19(10) ± 0.18	18.38(10) ± 1.31	85.65(10) ± 1.53	64.11(9) ± 3.48	44.20(10) ± 3.65
CONCIN	12.50(3) ± 0.50	3.67(3) ± 0.29	6.00(3)	15.50(3) ± 0.50	69.50(3) ± 3.91	55.33(3) ± 2.52	11.67(3) ± 0.58
CORALT	8.46(1)	3.54(1)	3.82(1)	17.98(1)	57.00(1)	29.00(1)	11.00(1)
CROSUL	27.92(3) ± 0.94	17.12(3) ± 1.78	8.90(3) ± 0.09	37.21(3) ± 3.67	131.67(3) ± 5.86	169(2) ± 8.49	70.00(3) ± 1.73

CYACYA	19.31(6) ± 0.89	13.30(6) ± 0.40	9.20(6) ± 0.58	23.74(6) ± 0.78	80.08(6) ± 2.58	67.00(1)	31.00(6) ± 2.37
DACVEN	11.33(1)	3.77(1)	3.87(1)	18.93(1)	65.00(1)	41.00(1)	18.00(1)
DENFUL	27.44(5) ± 0.11	6.90(5) ± 0.31	6.52(5) ± 0.34	26.79(5) ± 1.33	106.60(5) ± 3.05	83.80(5) ± 9.44	42.20(5) ± 1.79
DENSAN	36.00(8) ± 2.03	8.18(8) ± 0.36	9.06(8) ± 0.42	30.82(8) ± 1.60	124.31(8) ± 4.64	110.33(8) ± 4.20	69.75(8) ± 3.49
ELAFLA	11.04(7) ± 0.44	3.96(7) ± 0.19	4.90(7) ± 0.14	23.36(7) ± 1.30	78.29(7) ± 2.04	71.79(7) ± 3.46	24.43(7) ± 1.51
ELEPLA	34.33(1)	10.06(1)	14.67(1)	19.89(1)	109.00(1)	178.00(1)	51.00(1)
EMPALB	11.47(2) ± 0.52	3.61(2) ± 0.44	5.43(2) ± 0.18	16.21(2) ± 4.54	64.25(2) ± 13.08	54.00(2) ± 4.24	11.50(2) ± 2.12
EUPGOU	7.86(4) ± 2.29	4.24(4) ± 1.28	3.82(4) ± 1.15	12.74(4) ± 5.43	52.88(4) ± 1.49	24.75(4) ± 0.96	12.50(4) ± 1.00
EUPHIR	9.39(13) ± 0.38	5.49(13) ± 0.45	5.06(13) ± 0.47	17.26(13) ± 1.21	60.65(13) ± 2.79	34.85(10) ± 1.94	14.48(13) ± 1.06
EUPLUT	8.28(4) ± 0.86	4.58(4) ± 0.67	4.64(4) ± 0.19	17.38(4) ± 0.66	55.38(4) ± 1.89	32.00(2) ± 1.41	11.00(4) ± 2.00
FLOMEL	20.24(5) ± 3.83	2.42(5) ± 0.11	3.14(5) ± 0.22	4.82(5) ± 0.73	66.50(5) ± 1.58	34.40(5) ± 1.14	7.20(5) ± 0.45
GEOPOL	12.20(14) ± 0.66	4.50(14) ± 0.49	4.51(14) ± 2.65	24.74(14) ± 1.93	53.54(14) ± 8.45	57.67(12) ± 3.70	14.32(14) ± 1.17
GEOMON	11.77(1) ± 1.08	4.59(2) ± 0.13	3.64(2) ± 0.52	28.93(2) ± 1.03	140.00(2)	85.00(1)	133.50(2) ± 19.09
HELLON	33.66(2) ± 1.19	2.60(2) ± 0.42	3.16(2) ± 0.06	4.84(2) ± 0.23	58.00(2) ± 1.41	29.50(2) ± 2.12	6.00(2)
HENLEU	13.58(8) ± 3.76	3.12(8) ± 0.85	3.00(8) ± 0.80	22.96(8) ± 6.45	54.38(8) ± 2.80	25.43(7) ± 2.15	17.14(7) ± 0.90
HYLDEC	11.71(4) ± 0.39	3.56(4) ± 0.11	3.28(4) ± 0.16	19.42(4) ± 0.73	50.88(4) ± 2.69	33.13(4) ± 1.31	9.00(4) ± 0.82
ICTPRO	17.50(1)	5.50(1)	5.00(1)	26.00(1)	78.00(1)	85.00(1)	26.00(1)
LEPSOU	26.65(6) ± 0.83	5.00(6) ± 0.06	4.34(6) ± 0.22	21.09(6) ± 0.68	91.25(6) ± 3.74	76.75(4) ± 4.03	27.70(5) ± 1.31
LEPSUP	12.00(1)	3.80(1)	4.20(1)	17.00(1)	60.50(1)	56.00(1)	13.00(1)
LEPVER	17.79(3) ± 0.84	4.27(3) ± 0.25	3.82(3) ± 0.28	28.75(3) ± 7.52	139.00(3) ± 2.65	110.00(2) ± 1.41	158.00(3) ± 7.21
MANCAN	10.39(26) ± 1.81	3.70(26) ± 0.68	4.14(26) ± 0.78	22.87(26) ± 4.37	55.96(26) ± 2.34	36.23(22) ± 1.52	18.29(26) ± 1.49
MELHOF	23.00(1)	7.00(1)	7.50(1)	25.00(1)	119.00(1)	55.00(1)	65.00(1)
MELBIA	13.22(12) ± 0.70	7.35(12) ± 0.30	5.65(12) ± 0.37	27.67(12) ± 2.97	65.63(12) ± 2.66	60.06(8) ± 2.60	25.92(12) ± 2.75
MICMAR	18.55(2) ± 0.07	3.95(2) ± 0.07	3.95(2) ± 0.07	27.40(2) ± 0.57	59.75(2) ± 1.06	21.00(1)	20.00(2) ± 1.41
MICALB	10.99(1)	1.52(1)	2.29(1)	3.71(1)	42.50(1)	19.00(1)	2.00(1)
MIOOLE	11.67(26) ± 0.56	3.51(26) ± 0.25	4.28(26) ± 0.30	18.08(26) ± 1.31	62.75(26) ± 3.08	48.86(11) ± 2.70	13.42(26) ± 1.24
MITCAS	19.00(1)	7.30(1)	5.40(1)	27.50(1)	85.00(1)	75.00(1)	39.00(1)
MOMCOE	37.10(1)	12.62(1)	10.31(1)	35.49(1)	142.00(1)	227.00(1)	127.00(1)

MYITUB	16.19(11) ± 3.18	4.66(11) ± 0.79	6.81(11) ± 1.08	20.18(11) ± 4.08	70.77(11) ± 19.14	64.88(9) ± 21.89	18.82(11) ± 2.04
MYILUT	21.00(1)	9.00(1)	10.00(1)	23.50(1)	109.00(1)		44.80(1)
MYISIM	12.95(11) ± 0.77	4.91(11) ± 0.29	5.27(11) ± 0.34	20.96(11) ± 3.59	84.59(11) ± 2.67	66.00(3) ± 2.65	27.39(11) ± 1.28
MYREXS	20.55(4) ± 0.59	5.02(4) ± 0.05	5.08(4) ± 0.20	32.09(4) ± 2.34	66.38(4) ± 2.06	47.00(4) ± 1.15	27.75(4) ± 1.26
NYCALB	10.82(1)	3.65(1)	3.92(1)	27.40(1)	153.00(1)	140.00(1)	60.00(1)
ONCCIN	8.37(4) ± 3.07	2.69(4) ± 1.02	3.06(4) ± 1.22	12.23(4) ± 4.75	40.25(4) ± 6.85	29.88(4) ± 0.25	6.75(4) ± 0.50
ORYFUN	12.64(8) ± 0.41	9.74(8) ± 0.40	6.78(8) ± 0.25	18.42(8) ± 2.21	55.19(8) ± 2.28	49.25(4) ± 0.50	12.95(8) ± 0.83
PACCIN	12.89(2) ± 0.09	5.41(2) ± 0.16	7.27(2) ± 0.46	23.16(2) ± 0.28	75.50(2) ± 2.12	56.50(2) ± 2.12	22.00(2)
PACPOL	15.45(4) ± 3.04	5.85(4) ± 0.51	7.11(4) ± 1.10	22.70(4) ± 0.92	70.25(4) ± 3.07	53.33(3) ± 1.53	22.00(4) ± 3.37
PHALON	35.39(9) ± 6.44	2.80(9) ± 0.62	3.26(9) ± 0.75	4.31(8) ± 1.09	60.11(8) ± 2.41	65.39(9) ± 4.86	6.43(7) ± 0.53
PHASTR	21.22(20) ± 2.59	2.02(20) ± 0.25	2.57(20) ± 0.33	4.04(20) ± 0.45	39.93(20) ± 1.14	35.46(14) ± 2.02	2.67(18) ± 0.49
PHEATR	20.33(2) ± 2.84	4.99(2) ± 0.22	4.38(2) ± 0.25	27.68(2) ± 1.17	68.50(2) ± 0.71	57.00(2)	27.50(2) ± 2.12
PICSIM	20.00(1)	6.00(1)	7.50(1)	23.00(1)	111.00(1)	59.00(1)	55.00(1)
PIOSEN	29.50(1)	23.00(1)	14.50(1)	32.50(1)	182.50(1)	73.50(1)	206.00(1)
PITSUL	27.48(4) ± 2.15	9.64(4) ± 0.86	11.69(4) ± 2.46	25.90(4) ± 3.47	116.25(4) ± 3.59	86.13(4) ± 3.28	64.75(4) ± 2.22
POLPLU	11.66(13) ± 0.56	2.44(13) ± 0.11	2.98(13) ± 0.27	18.43(13) ± 0.86	45.50(13) ± 1.79	37.83(6) ± 1.72	6.15(13) ± 0.38
PROCHA	6.29(1)	2.39(1)	2.99(1)	11.20(1)	94.00(1)	51.00(1)	10.00(1)
PSAMON	59.33(3) ± 3.15	16.77(3) ± 2.04	10.76(3) ± 1.09	54.45(3) ± 3.94	187.33(3) ± 8.08	56.30(3) ± 71.62	217.33(3) ± 12.22
PTETOR	85.55(6) ± 24.89	26.01(6) ± 8.19	21.43(6) ± 6.79	29.14(6) ± 8.86	145.33(6) ± 5.16	154.67(6) ± 5.61	201.67(6) ± 16.59
QUIMEX	42.53(2) ± 0.17	12.92(2) ± 0.95	9.72(2) ± 0.67	60.53(2) ± 0.81	181.50(2) ± 2.12	193.50(2) ± 6.36	220.00(2) ± 5.66
RAMSUL	134.50(1)	43.50(1)	33.50(1)	56.50(1)	200.00(1)		438.00(1)
RAMMEL	22.74(4) ± 0.27	2.95(4) ± 0.06	2.81(4) ± 0.22	24.47(4) ± 0.63	51.25(4) ± 1.50	42.25(2) ± 1.06	10.50(4) ± 0.58
RAMPAS	14.81(8) ± 1.34	7.25(8) ± 0.23	7.12(8) ± 0.25	25.50(8) ± 1.79	74.06(8) ± 2.77	65.50(8) ± 4.04	30.25(8) ± 1.67
RUPMAG	28.83(1)	13.97(1)	10.77(1)	69.24(1)	270.00(1)	147.00(1)	336.00(1)
SALCOE	19.00(1)	10.50(1)	8.50(1)	31.00(1)	96.00(1)	90.00(1)	51.00(1)
SALMAX	20.16(12) ± 1.01	9.91(12) ± 0.88	8.59(12) ± 0.92	28.47(12) ± 3.44	98.54(12) ± 3.65	93.25(12) ± 3.79	47.25(12) ± 2.49
SPOCOR	9.54(24) ± 0.40	7.14(24) ± 0.22	5.26(24) ± 0.29	18.32(24) ± 0.79	51.28(24) ± 8.68	43.33(6) ± 1.97	11.46(23) ± 0.79
SPOTOR	8.91(16) ± 0.47	6.58(16) ± 0.52	5.20(16) ± 0.60	17.05(16) ± 0.92	49.72(16) ± 1.71	42.04(13) ± 3.28	8.93(16) ± 0.75

STESER	6.85(7) ± 0.53	2.66(7) ± 0.38	3.43(7) ± 0.48	11.62(6) ± 1.31	97.93(7) ± 18.53	47.20(5) ± 2.95	14.43(7) ± 0.53
STUMAG	32.56(1)	8.56(1)	6.14(1)	46.89(1)	100.50(1)	53.00(1)	93.00(1)
STUMIL	12.85(2) ± 5.41	5.24(2) ± 2.31	4.00(2) ± 2.05	22.08(2) ± 9.71	78.50(2) ± 0.71	51.50(2) ± 0.71	31.50(2) ± 2.12
TACLUC	13.22(4) ± 0.49	5.82(4) ± 0.22	5.10(4) ± 0.14	19.30(4) ± 0.95	61.25(4) ± 0.96	47.25(4) ± 14.93	14.50(4) ± 0.58
TACRUF	18.11(1)	7.54(1)	6.73(1)	26.57(1)	85.00(1)	53.00(1)	34.00(1)
TANINO	13.55(1)	6.29(1)	5.43(1)	21.41(1)	91.50(1)	67.00(1)	37.00(1)
TANLAR	10.60(11) ± 1.61	5.08(11) ± 0.39	4.64(11) ± 0.52	20.21(11) ± 1.93	71.68(11) ± 6.61	49.18(11) ± 7.07	20.09(11) ± 6.07
TERERY	8.90(1)	2.50(1)	4.00(1)	17.00(1)	49.00(1)	37.00(1)	8.00(1)
THACOL	20.13(5) ± 0.63	1.96(5) ± 0.04	2.79(5) ± 0.22	4.18(4) ± 1.15	54.30(5) ± 1.64	36.75(4) ± 4.03	4.25(4) ± 0.50
THAATR	18.95(10) ± 2.02	6.55(10) ± 0.35	5.68(10) ± 0.70	24.58(10) ± 1.04	68.50(10) ± 2.77	55.11(9) ± 1.83	24.35(10) ± 2.03
THADOL	19.16(2) ± 3.05	6.65(2) ± 0.21	5.86(2) ± 0.21	30.74(2) ± 1.08	69.75(2) ± 0.35	62.00(2) ± 2.83	27.00(2)
THREPI	12.46(16) ± 2.34	6.27(16) ± 1.24	5.94(16) ± 1.31	23.12(15) ± 1.34	87.13(16) ± 3.00	63.20(15) ± 1.86	32.52(15) ± 2.50
THRPAL	12.91(2) ± 0.83	6.24(2) ± 0.37	5.77(2) ± 0.33	24.03(2) ± 2.79	90.00(2) ± 1.41	66.50(2) ± 0.71	35.50(2) ± 3.54
TIAOLI	9.64(30) ± 0.37	5.77(30) ± 0.36	4.17(30) ± 0.27	19.54(30) ± 0.52	49.13(30) ± 1.77	40.00(8) ± 2.63	9.93(30) ± 0.75
TODCIN	13.40(13) ± 0.73	2.92(13) ± 0.17	4.78(13) ± 0.20	19.92(13) ± 0.92	41.92(13) ± 1.19	31.83(9) ± 1.70	6.38(13) ± 0.65
TOLSUL	11.10(10) ± 2.06	3.34(10) ± 0.63	5.19(10) ± 0.87	19.74(10) ± 3.58	60.25(10) ± 7.63	51.55(10) ± 6.64	13.40(10) ± 3.13
TROAED	13.89(24) ± 2.45	3.02(23) ± 0.17	3.01(23) ± 0.27	21.08(22) ± 1.10	48.91(23) ± 1.86	34.80(10) ± 2.24	11.87(23) ± 0.81
TURGRA	20.24(11) ± 1.20	6.51(11) ± 0.39	5.81(11) ± 0.64	36.75(11) ± 1.73	116.82(11) ± 4.52	96.60(5) ± 4.83	72.82(11) ± 5.12
TYRMEL	21.28(5) ± 0.75	7.31(5) ± 0.15	9.87(5) ± 0.26	21.35(5) ± 1.79	111.80(5) ± 2.68	92.20(5) ± 1.64	44.40(5) ± 3.36
VANCHI	30.50(2) ± 0.81	7.83(2) ± 0.49	7.62(2) ± 0.85	81.50(2) ± 3.10	234.00(2) ± 1.41	98.50(2) ± 3.54	258.50(2) ± 28.99
VIRFLA	13.57(1)	4.45(1)	4.45(1)	18.39(1)	74.50(1)	50.00(1)	17.00(1)
VOLJAC	9.86(44) ± 0.48	5.18(44) ± 0.42	4.08(44) ± 0.27	16.97(44) ± 1.69	47.15(44) ± 1.30	38.65(10) ± 2.65	9.53(44) ± 0.53
XENMIN	12.29(5) ± 0.53	4.52(5) ± 0.12	3.73(5) ± 0.22	16.56(5) ± 0.66	59.50(5) ± 2.78	45.50(5) ± 3.21	11.80(5) ± 1.10
XIPSUS	32.47(7) ± 7.22	6.32(7) ± 1.42	5.28(7) ± 1.26	23.22(7) ± 5.21	101.00(7) ± 5.14	85.67(6) ± 5.35	43.71(7) ± 4.79
ZIMVIL	7.31(8) ± 1.77	2.97(8) ± 0.70	3.18(8) ± 0.76	18.11(8) ± 4.76	48.31(8) ± 2.75	37.29(7) ± 3.85	8.25(8) ± 1.28

Table S2. List of Latin and English names of bird species for which functional traits have been measured.

#	Latin name	English name	Species Code
1	*Amazilia tzacatl*	Rufous-tailed Hummingbird	AMATZA
2	*Amblycercus holosericeus*	Yellow-billed Cacique	AMBHOL
3	*Anthracothorax prevostii*	Green-breasted Mango	ANTPRE
4	*Arremonops conirostris*	Black-striped Sparrow	ARRCON
5	*Attila spadiceus*	Bright-rumped Attila	ATTSPA
6	*Automolus ochrolaemus*	Buff-throated Foliage-gleaner	AUTOCH
7	*Baryphthengus martii*	Rufous Motmot	BARMAR
8	*Basileuterus rufifrons*	Rufous-capped Warbler	BASRUF
9	*Butorides virescens*	Green Heron	BUTVIR
10	*Campylopterus hemileucurus*	Violet Sabrewing	CAMPHEM
11	*Cantorchilus modestus*	Plain Wren	CANMOD
12	*Cartorchilus nigricapillus*	Bay Wren	CANNIG
13	*Cercomacra tyrannina*	Dusky Antbird	CERTYR
14	*Coereba flaveola*	Bananaquit	COEFLA
15	*Colibri thalassinus*	Green Violetear	COLTHA
16	*Columbina minuta*	Plain-breasted Ground-Dove	COLMIN
17	*Columbina talpacoti*	Ruddy Ground-Dove	COLTAL
18	*Contopus cinereus*	Tropical Pewee	CONCIN
19	*Corapipo altera*	White-ruffed Manakin	CORALT
20	*Crotophaga sulcirostris*	Groove-billed Ani	CROSUL
21	*Cyanocompsa cyanoides*	Blue-black Grosbeak	CYACYA
22	*Dacnis venusta*	Scarlet-thighed Dacnis	DACVEN
23	*Dendrocincla fuliginosa*	Plain-brown Woodcreeper	DENFUL
24	*Dendrocolaptes sanctithomae*	Northern Barred-Woodcreeper	DENSAN
25	*Elaenia flavogaster*	Yellow-billed Elaenia	ELAFLA
26	*Electron platyrhynchum*	Broad-billed Motmot	ELEPLA
27	*Empidonax albigularis*	White-throated Flycatcher	EMPALB
28	*Euphonia gouldi*	Olive-backed Euphonia	EUPGOU
29	*Euphonia hirundinacea*	Yellow-throated Euphonia	EUPHIR
30	*Euphonia luteicapilla*	Yellow-crowned Euphonia	EUPLUT
31	*Florisuga mellivora*	White-necked Jacobin	FLOMEL
32	*Geothlypis poliocephala*	Gray-crowned Yellowthroat	GEOPOL
33	*Geotrygon montana*	Ruddy Quail-Dove	GEOMON
34	*Heliomaster longirostris*	Long-billed Starthroat	HELLON

35	*Henicorhina leucosticta*	White-breasted Wood-Wren	HENLEU
36	*Hylophilus decurtatus*	Lesser Greenlet	HYLDEC
37	*Icterus prosthemelas*	Black-cowled Oriole	ICTPRO
38	*Lepidocolaptes souleyetii*	Streak-headed Woodcreeper	LEPSOU
39	*Leptopogon superciliaris*	Slaty-capped Flycatcher	LEPSUP
40	*Leptotila verreauxi*	White-tipped Dove	LEPVER
41	*Manacus candei*	White-collared Manakin	MANCAN
42	*Melanerpes hoffmannii*	Hoffmann's Woodpecker	MELHOF
43	*Melozone biarcuata*	Prevost's Ground-Sparrow	MELBIA
44	*Microcerculus marginatus*	Scaly-breasted Wren	MICMAR
45	*Microchera albocoronata*	Snowcap	MICALB
46	*Mionectes oleagineus*	Ochre-bellied Flycatcher	MIOOLE
47	*Mitrospingus cassinii*	Dusky-faced Tanager	MITCAS
48	*Momotus coeruliceps*	Blue-crowned Motmot	MOMCOE
49	*Myiarchus tuberculifer*	Dusky-capped Flycatcher	MYITUB
50	*Myiodynastes luteiventris*	Sulphur-bellied Flycatcher	MYILUT
51	*Myiozetetes similis*	Social Flycatcher	MYISIM
52	*Myrmeciza exsul*	Chestnut-backed Antbird	MYREXS
53	*Nyctidromus albicollis*	Common Pauraque	NYCALB
54	*Oncostoma cinereigulare*	Northern Bentbill	ONCCIN
55	*Oryzoborus funereus*	Thick-billed Finch	ORYFUN
56	*Pachyramphus cinnamomeus*	Cinnamon Becard	PACCIN
57	*Pachyramphus polychopterus*	White-winged Becard	PACPOL
58	*Phaethornis longirostris*	Long-billed Hermit	PHALON
59	*Phaethornis striigularis*	Stripe-throated Hermit	PHASTR
60	*Pheugopedius atrogularis*	Black-throated Wren	PHEATR
61	*Piculus simplex*	Rufous-winged Woodpecker	PICSIM
62	*Pionus senilis*	White-crowned Parrot	PIOSEN
63	*Pitangus sulphuratus*	Great Kiskadee	PITSUL
64	*Polioptila plumbea*	Tropical Gnatcatcher	POLPLU
65	*Progne chalybea*	Gray-breasted Martin	PROCHA
66	*Psarocolius montezuma*	Montezuma Oropendola	PSAMON
67	*Pteroglossus torquatus*	Collared Aracari	PTETOR
68	*Quiscalus mexicanus*	Great-tailed Grackle	QUIMEX
69	*Ramphastos sulfuratus*	Keel-billed Toucan	RAMSUL
70	*Ramphocaenus melanurus*	Long-billed Gnatwren	RAMMEL
71	*Ramphocelus passerinii*	Passerini's Tanager	RAMPAS
72	*Rupornis magnirostris*	Roadside Hawk	RUPMAG
73	*Saltator coerulescens*	Grayish Saltator	SALCOE

74	*Saltator maximus*	Buff-throated Saltator	SALMAX
75	*Sporophila corvina*	Variable Seedeater	SPOCOR
76	*Sporophila torqueola*	White-collard Seedeater	SPOTOR
77	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow	STESER
78	*Sturnella magna*	Eastern Meadowlark	STUMAG
79	*Sturnella militaris*	Red-breasted Blackbird	STUMIL
80	*Tachyphonus luctuosus*	White-shouldered Tanager	TACLUC
81	*Tachyphonus rufus*	White-lined Tanager	TACRUF
82	*Tangara inornata*	Plain-colored Tanager	TANINO
83	*Tangara larvata*	Golden-hooded Tanager	TANLAR
84	*Terenotriccus erythrurus*	Ruddy-tailed Flycatcher	TERERY
85	*Thalurania colombica*	Crowned Woodnymph	THACOL
86	*Thamnophilus atrinucha*	Black-crowned Antshrike	THAATR
87	*Thamnophilus doliatus*	Barred Antshrike	THADOL
88	*Thraupis episcopus*	Blue-gray Tanager	THREPI
89	*Thraupis palmarum*	Palm Tanager	THRPAL
90	*Tiaris olivaceus*	Yellow-faced Grassquit	TIAOLI
91	*Todirostrum cinereum*	Common Tody-Flycatcher	TODCIN
92	*Tolmomyias sulphurescens*	Yellow-olive Flycatcher	TOLSUL
93	*Troglodytes aedon*	House Wren	TROAED
94	*Turdus grayi*	Clay-colored Thrush	TURGRA
95	*Tyrannus melancholicus*	Tropical Kingbird	TYRMEL
96	*Vanellus chilensis*	Southern Lapwing	VANCHI
97	*Vireo flavoviridis*	Yellow-green Vireo	VIRFLA
98	*Volatinia jacarina*	Blue-black Grassquit	VOLJAC
99	*Xenops minutus*	Plain Xenops	XENMIN
100	*Xiphorhynchus susurrans*	Cocoa Woodcreeper	XIPSUS
101	*Zimmerius vilissimus*	Paltry Tyrannulet	ZIMVIL

Chapter 2. Stable landscapes help maintain stable bird communities

Abstract

Forest conversion to agriculture remains a major threat to biodiversity conservation. Land use practices in Central America have produced a variety of studies that are focused towards avian conservation. In order to expand upon our understanding of how land use practices influence avian conservation, we aimed to evaluate inter- and intra-annual avian community change over a seven year period in land uses predominant within the Volcanica Central Talamanca Biological Corridor (VCTBC) in Costa Rica. We selected eight land uses following a management intensity gradient from forests to sugar cane to test impacts of land-use cascade effects. Using captured data from long-term mist-netting stations we found that the majority of monitored land uses are capable of supporting stable bird communities. Stability understood as no changes from year to year in mean species richness and abundance of either the total population, or of resident and migratory species over a seven-year period. We also found that the forest land use has a unique bird community composition when compared to other land uses, and that agroforest land uses such as multi strata coffee agroforest, multi strata cacao agroforest and simplified coffee agroforest had similar composition between them but distinct from forest and from the more intensively managed land uses. Our findings provide further evidence on the land-use cascade effect as composition of bird communities changed as we moved in a gradient of management intensification highlighting the importance of forest fragments, remaining in agricultural landscapes, for the persistence of bird species of conservation concern.

Resumen

La conversión de áreas boscosas a tierras agrícolas continúa siendo la mayor amenaza para la conservación de la biodiversidad. Las prácticas de uso de suelo en Centroamérica han generado una serie de estudios enfocados en la conservación de las aves silvestres. Con el objetivo de ampliar nuestro conocimiento sobre el efecto de diferentes usos de suelo sobre la conservación de estas especies, nos propusimos evaluar cambios inter- e intra-anuales en comunidades de aves en usos de suelo predominantes en el Corredor Biológico Volcánica Central Talamanca (CBVCT) en Costa Rica. Seleccionamos ocho usos de suelo siguiendo un gradiente de intensificación y utilizando datos de capturas provenientes de estaciones de anillamiento permanentes, encontramos que la mayoría de los usos de suelo estudiados son capaces de mantener comunidades estables. Estabilidad definida como la ausencia de cambios de un año a otro en el promedio de la riqueza de especies y abundancia, de la población total o de las poblaciones residentes y/o migratorias durante un período de siete años. Los resultados muestran que el bosque alberga una comunidad única, y que usos de suelo agroforestales como el café y cacao multiestrato y el café simplificado albergan comunidades similares entre ellos pero distintas del bosque y de los usos de suelo bajo un manejo más intensivo. Estos hallazgos proveen evidencia adicional sobre los efectos en cascada de diferentes usos de suelo, resaltando la importancia de fragmentos de bosques remanentes en paisajes agrícolas para la permanencia de especies de interés para la conservación.

Key words: Mist-netting, Biological Corridors, Long-term monitoring, agricultural land uses, agroforestry

Introduction

Forest conversion to agriculture remains a major threat to biodiversity conservation. Expansion of agricultural lands, particularly in highly diverse regions such as the American tropics (Myers *et al.* 2000), has prompted more than 20 years of research to understand the habitat and conservation value of alternate agricultural land use and their configuration in mosaic landscapes (Pimentel *et al.* 1992, Vandermeer and Perfecto 1997, Liu *et al.* 2001, Dirzo and Raven 2003, Harvey *et al.* 2006, Sekercioglu *et al.* 2007, Gardner *et al.* 2009, DeClerck *et al.* 2010).

Conservation value of agricultural lands is highly dependent on management decisions, especially for bird communities. Intensively managed land uses usually show lower bird species richness and abundance when compared to other less intense managed land use types (Petit and Petit 2003, Luck and Daily 2003, Flynn *et al.* 2009). For instance, Petit *et al.* (1999) compared bird communities across eleven different land use types, and found that avian community composition in coffee agroforests shared 43% of the avian composition found in lowland forest fragments while sugar cane plantations were more similar to rice fields sharing 60% of bird species. Different studies have shown that embedding conservation structures in agricultural landscapes, such as agroforests, are a feasible alternative to balancing food production and biodiversity conservation (McNeely and Schroth 2006, Harvey and González 2007, Van Bael *et al.* 2007). However, management decisions affect the conservation value of these systems (Perfecto *et al.* 1996, Greenberg *et al.* 1997a, 1997b, Greenberg *et al.* 2000) as well as their capacity to deliver important ecosystem services (Kellermann *et al.* 2008, Johnson *et al.* 2010, Karp *et al.* 2013, Maas *et al.* 2013, Maas *et al.* 2015).

Proximity of important habitat elements may also influence the response of different animal taxa. Ricketts *et al.* (2001) found no significant difference in moth species richness and abundance when considering native forests and agricultural habitats such as coffee (shaded and non-shaded), pastures and mixed farms but did find an effect of forest proximity on moth richness, abundance and composition, with higher richness and abundance in agricultural sites in close proximity to forest fragments. Ricketts (2004) found similar results for wild bee populations, with greater species richness and pollination rates in coffee plantations proximate to forest fragments. Additionally, Ricketts (2004) found that both species richness and pollen deposition rates dropped with increasing distance to forest fragments.

Land use practices in Central America have produced a variety of studies that are focused towards avian conservation (Petit *et al.* 1999, Petit and Petit 2003, Lindell *et al.* 2003, Harvey *et al.* 2006, Hernández *et al.* 2013, Vílchez-Mendoza *et al.* 2014), and these studies are typically conducted over a 1-4 year time span. Karp *et al.* (2011) have noted that longer duration studies will facilitate a better understanding of how land use and other environmental factors might affect avian communities. Both inter- and intra-annual studies in avian communities as a function of land use are relatively rare (Luck and Daily 2003, Lindell *et al.* 2004, Karp *et al.* 2011) and much needed to better understand community dynamics and trends. Additionally, most studies do not consider potential influences from larger conservation initiatives where their studies are nested (but see Fagan *et al.* 2016). In Costa Rica, these can include national scale conservation efforts such as biological corridors, whose main goal is to foster connectivity and habitat protection for biodiversity and which may exhibit different degrees of success.

In order to expand upon our understanding of how land use practices in Central America influence avian conservation, we aimed to evaluate inter- and intra-annual avian community change over a seven year period within the Volcanica Central Talamanca Biological Corridor (VCTBC). This is a longer and more temporally dense approach than has been previously noted in other studies (Lindell *et al.* 2003, Hernández *et al.* 2013). We selected eight land uses (Fig. 1) the majority of which are largely predominant within the biological corridor. Selected land uses follow a management intensity gradient from forests to sugar cane to test impacts of land-use cascade effects (Terborgh and van Schaik 1996, Phalan *et al.* 2011). The cascade effect hypothesizes that shifting from a less to a more intensive land use management will often have detrimental impacts on wild species. Avian communities in tropical ecosystems are subject to many different pressures (Tobias *et al.* 2013) including those related to land use conversion and intensification. We consider avian communities occupying differently managed land uses within the VCTBC to test whether population change signals are attributable to distinct conservation pressures. Using a gradient of land use intensity we test: (1) whether resident and migratory bird species richness and abundance have changed over time, and (2) whether community similarity changed within and across selected land uses over a seven year period.

The VCTBC is a conservation initiative supported by the Costa Rican government whose main goal is to re-establish connectivity between the Volcanica Central and the Talamanca mountain ranges (Canet 2008). The VCTBC is embedded within the Mesoamerican Biological Corridor, a regional biodiversity connectivity and conservation initiative which recognizes the central role of local populations as agents of conservation action and land use change (DeClerck *et al.* 2010). The VCTBC is an example of land sharing

(Phalan *et al.* 2011) at the landscape level, as it concentrates production and conservation efforts in a relatively small territory. Because of its duration (seven years), and observation of multiple land uses (eight land uses) and high temporal resolution (monthly surveys), this study provides an additional perspective to existing studies relating to the land-use cascade effect and the temporal characteristics of bird communities in the context of national conservation strategies such as biological corridors.

Methods

Study area

The study was conducted in the Turrialba region of Costa Rica, Central America, primarily on the Tropical Agricultural Research and Higher Education Center (CATIE) main campus and commercial farm. The CATIE property has an area of 1036 ha (lat 9°53' N, long 83°43' W) and encompasses a diversity of productive systems. The predominant land uses include forest, cattle pastures, sugar cane and coffee. CATIE is situated within the Caribbean watershed of Costa Rica at 600 m.a.s.l. and corresponds to the very humid pre-montane forest ecological zone. The average rainfall is 2636 mm, with mean temperature of 22°C and a relative humidity of 87% (CATIE meteorological station *unpublished data*). Rainfall is almost evenly distributed throughout the year but usually decreases between February and April. CATIE is one of the largest farms in the Turrialba valley combining different production activities such as pastures, sugar cane, coffee (*Coffea arabica* var. caturra), forests plantations and reforestation plots, nurseries and small organic agriculture plots. Additionally, the farm also includes approximately 200 ha of secondary forest and a botanical garden where several varieties of coffee, cacao, palms and other tropical species are kept.

CATIE is located at the heart of the 114,626 ha Volcanica Central Talamanca Biological Corridor (VCTBC). Over 50% of the corridor is covered by forests with more than 30% of the remaining area covered by agriculture. Pastures (25%), coffee (9%), shrublands (6%), and sugar cane (4%) being the most important land uses following forest. The VCTBC is a national conservation strategy established in 2003 aiming at reconnecting the Volcanica Central and the Talamanca mountain ranges (Canet 2008). The VCTBC is part of the National Biological Corridors Program managed by the Costa Rica National System of Conservation Areas (SINAC).

General description of selected land uses

Data were collected in eight different land uses within the CATIE campus and commercial farm. These land uses included: (1) a well-preserved mature secondary forest; (2) a multi-strata agroforestry coffee system associated with poró (*Erythrina poeppigiana*), a leguminous nitrogen-fixing tree and laurel (*Cordia alliodora*); (3) a simplified coffee agroforest exclusively associated with poró; (4) a multi-strata agroforestry cacao (*Theobroma cacao*) system associated with laurel and banana (*Musaceae sp.*); (5) pasture lands surrounded by live fences; (6) sugar cane (*Saccharum officinarum*); (7) a mixed species forest plantation which includes *Vochysia ferruginea*, *Eucalyptus sp*., *Cedrela sp.*; and (8) a teak (*Tectona grandis*) plantation (Fig. 1).

Land use complexity varied from mature secondary forests to simplified monocultures. Our forest site (FORE) corresponds to our reference system and it exhibits a well-developed understory and mid- and upper level canopy (Fig. 1a). FORE most abundant tree species included *Dendropanax aff. gonatopodus* (Araliaceae), *Spondias radlkoferi*

(Anacardiaceae), *Turpinia occidentalis* (Staphyleaceae), *Allophylus psilospermus* (Sapindaceae), *Lonchocarpus guatemalensis* (Fabaceae), *Terminalia oblonga* (Combretaceae) and *Hasseltia floribunda* (Salicaceae). Our two coffee sites differed in vertical structure complexity as one of them is in exclusive association with poró trees (SICO) representing the typical coffee system found in Costa Rica in which arrangement of plots correspond to coffee plants interspersed by poró trees whose branches are radically and regularly (usually twice a year) pruned (Fig. 1d). Poró is a very fast growing leguminous fixing tree, which allows for highly plastic canopy closure. The second coffee site, corresponds to an abandoned multi-strata agroforestry coffee plantation (MACO) (Fig. 1c). MACO was abandoned nearly 20 years ago, though its shrub strata is still dominated by coffee plants. It exhibits a well-defined middle strata consisting primarily of formerly pruned poró trees that now reach heights of about 12 m, and an upper strata dominated by laurel trees that can reach 20 m in height. The plot vegetation structure is equivalent to coffee sites managed for Smithsonian Bird Friendly standards which promote avian habitat conservation in coffee (DeClerck and Martínez-Salinas 2011). The multi-strata agroforestry cacao site (MACA) has a vegetation structure similar to our MACO site, but in this case cacao shrubs (2-3 m) dominate the understory, interspersed with banana plants and tree canopy height varies from 10 to 25 m (Fig. 1b). Our live fence site (LIFE) consists of a 300 m long linear row of trees dominated by *Inga* spp. and two species of poró (*E. poeppigiana* and *E. fusca*) (Fig. 1g). These trees form the boundary between pastures with live trees serving as fence posts to which barbed wire is affixed. Networks of fences can serve both as habitat and corridors for birds (Harvey *et al.* 2005). Pastures are dominated by Tanner grass (*Brachiaria radicans*) with management varying from regularly grazing to fallows of six months or less (particularly in 2010). The two

independent forest plantations sites consist of a mixed species (MSPL) (Fig. 1f) planted in 2008 and a pure teak plantation (TEPL) (Fig. 1e) planted in 2010 (replacing a portion of the MACO site). The system with the simplest vertical structure is sugar cane (SUCA). During sugar cane's production cycle, the plant can reach heights of 2.5 to 3 m, with approximately 1 m spacing between rows. The cane is burnt and harvested once a year, usually in May.

Sampling protocols

We used data from permanent mist netting stations. Stations were first established in January 2008 in all land use types except MSPL and TEPL where they were established in 2011. Originally, a total of ten mistnets were placed in each land use type, following standard protocols (Ralph *et al.* 1993). Distance between nets varied between 5-20 m depending on land use. Mistnets have standard dimensions (12 m long x 2.5 m height x 30 mm mesh size) recommended for passerine birds (Ralph *et al.* 1993). Operation of stations started at 0500 until 0900 with net checks every 40 minutes. Opening and closing times varied by ±30 minutes depending on weather conditions and season, all variations pertaining to sampling effort were recorded. During each net round captured birds were removed from nets and placed into individual cloth bags to reduce stress due to handling. They were then carried back to processing stations. All captured birds except hummingbirds and large species for which we did not have appropriate band sizes, were banded using numbered aluminum bands. Resident birds were fitted with Costa Rican Ornithological Association (AOCR) bands and migratory birds were fitted with US Geological Survey (USGS) bands provided under the Institute for Bird Populations (IBP) master bander permit following North American Banding Council (NABC) regulations. Our capture and handling procedures were in compliance with

national (Costa Rica Scientific Passport #04541) and international standards and regulations (IACUC protocol #2012-20).

Statistical analyses

We used Generalized Additive Mixed Models (GAMM) (Zuur *et al.* 2009) to explore significance of predictor variables on species richness and abundance over seven years of sampling. We used the abundance and richness measures of the resident, migratory, and total bird species communities in our assessment. We recorded land use type, sampling effort (mistnetting hours), month and time and their interactions as predictor variables. The time variable corresponded to the sampling date at which different land uses were sampled converted to a unique continuous numerical value. Predictor variables month and time capture the temporal variation (tendency) and seasonality of the data, both required in a time series analysis (Legendre and Legendre 2012). We designated month, time and effort as fixed effects and land use type as random effect. We constructed two types of models (1) using Negative Binomial distribution to address overdispersion of the data using splines as smoothing functions for single factors and interactions, and (2) using Zero Inflated Poisson distribution to address periods of migratory bird species absence and thus abundance of zero values using P-splines as smoothing functions for single factors and a tensor product for interactions. We evaluated adequacy of models through diagnostic graphs (R function gam.check, Fig. S1). Single factors and their interactions were considered to be significant when $P < 0.05$. Analyses were performed with mgcv R package (version 3.1.2) using the implemented interface in *InfoStat* (Di Rienzo *et al.* version 2015).

To address how community similarity might change over time we used ordination techniques. First, we used nonmetric MultiDimensional Scaling (nMDS) ordination technique to identify bird species associated to land uses with annual time steps tracked over the course of seven years (Fig. S5-S8). nMDS allows us "to plot dissimilar objects far apart in the ordination space and similar objects close to one another" (p. 512, Legendre and Legendre 2012). We used Hellinger transformation (Legendre and Gallager 2001) and Euclidean distance. A total of six dimensions were required to obtain a final stress value around 10 or < 10. The stress value is an indication of goodness of fit of the analysis (Legendre and Legendre 2012). Using the results from Pearson correlations between bird species and eigenvectors from the nMDS, we identified bird species associated with our different sampling units within land use types by selecting bird species with correlation coefficients > 0.30 or < -0.30. According to Cohen (1988) correlations values of 0.30 show a moderate strength. Finally, we conducted a Generalised Procrustes Analysis (GPA) based on nMDS eigenvector values calculated for each year and each land use from 2008 to 2014. The GPA analysis allowed us to compare the ordinations (Wieringa *et al.* 2009) and we thus obtained a general consensus on bird community changes over time. Community similarity analyses were performed using *InfoStat* software (Di Rienzo *et al.* version 2015).

Results

General results

From January 2008 through December 2014, a total of 8,750 birds were captured and evaluated as part of our monitoring efforts. Monitoring efforts included a total of 769 sampling dates and 19,446 net hours (Table 1). The 8,750 individuals belong to 205 bird species distributed amongst 31 families (Table S1); 82% of all birds were classified as resident bird species while Neotropical migrants accounted for the remaining 18% of all captured individuals (Table 1). The most species diverse family was Tyrannidae with 34 species and the family with the highest abundance was Emberizidae representing a total of 11 species and a 28% of all captured individuals (n = 2,482). Rufous-tailed Hummingbird *Amazilia tzacatl*, was our most common capture with 1,198 individuals (14%), followed by Variable Seedeater *Sporophila corvina* with 938 (11%) individuals. Overall, the ten most common bird species accounted for over 50% of all individuals trapped (Table 2).

Overall temporal patterns

Land use type, month and effort were all significant predictors of species richness and abundance, of either the total population, or of resident and migratory species (Table 3). Interaction between Time and Month was significant at reflecting changes in migratory community metrics over our seven year sampling period (Table 3).

Bird species richness

Within year patterns show variations in the number of bird species captured across land use types. However, mean species richness remained stable across years for the majority

of land uses except MACO and SICO (Fig. 2a), where a downward and upward trend is observed respectively (Fig. S2a, b). Decreasing patterns at our MACO land use are the result of higher capture rates in our first years of operation with 14 bird species captured in 2008, 14 bird species captured between 2008 and 2009 (63 ± 1.41), and an additional 3 bird species captured between 2008, 2009 and 2010 (57 ± 10.44) that were not re-captured in subsequent years. Additionally, in October 2010 our MACO land use was subject to severe interventions which destroyed half our sampling area. Since 2011, mean species richness have stabilize with an annual average of 29 ± 5.35 species captured. Increasing patterns in our SICO land use are a result of higher captures during the years 2010, 2011 and 2012 with an average of 61 ± 1.53 species captured annually compared to the overall average of 54 ± 7.78 species captured during the 2008-2014 period. Finally, monthly patterns of overall species richness show for all land use types a decrease in mean species richness during the April-September period, this pattern is more evident in the SICO and LIFE (Fig. 2b) land uses.

Yearly patterns of resident and migratory species richness (Fig. 3a, c) show stability of bird communities for the majority of land use types. Mean resident species richness (Fig. 3a) follow the same patterns observed in overall species richnes (Fig. 2a) where the majority of land uses show stability across years with the exception of the MACO and SICO land uses. Downward and upward trends observed in the overall species richness at the MACO and SICO land uses (Fig. S2a, b) are result of the predominant trends within the resident community (Fig. 3a) these trends being absent from the migratory community. Resident species richness in the remaining land uses, fluctuates within years and across land use types but remains stable across years within land uses (Fig. 3a). Monthly patterns of resident species richness show a slight decrease across land use types as we move from the beginning

to the end of the year (Fig. 3b). This decrease pattern is particularly evident in our MACO land use where differences in capture rates in our first three years of sampling (2008, 2009 and 2010) are driving these trends (Fig. S3). Additionally, mean migratory species richness yearly patterns show overall stability across years and land use types (Fig. 3c). Monthly patterns on the other hand exhibit a reduction in mean species richness during the April-September period (Fig. 3d). This reduction also observed in the overall species richness (Fig. 2a) is consistent with absence of migratory species due to migration events.

Bird abundance

Overall mean bird abundance remained stable across years for most sampling units within land use types except for TEPL, MACO and SICO. TEPL exhibits a steep increase in bird abundance since plantation establishment in November 2011, which is consistent with an increase in sampling dates in subsequent years as well as changes in understory and treee growth which may facilitate movement of birds thus increasing numbers of birds captured (Fig. S4). MACO and SICO patterns of overall abundance (Fig. 4a) coincide with trends previously observed for overall species richness (Fig. 2a). MACO average annual capture rates in our first three years of operation (2008-2010) was 275 ± 132.86 individuals compared to the 84 ± 27.89 in subsequent years (2011-2014) which clearly indicates a drop in capture rates (Fig. S4). SICO on the other hand exhibits a more variable abundance capture rate with a mean abundance showing the opposite trend than MACO. Upward trend observed in our SICO land use is driven particularly by greater number of birds captured in the year 2011 (n = 588) compared to other years (Fig. S4). Additionally, monthly trends of overall mean bird abundance show stability across years for most land uses with the exception of SICO where a

slight downward trend is observed consistent with the trend present for monthly mean resident species richness (Fig. 3b). The greatest overall species abundance is observed at our SICO land use, probably a result of this land use simplified vertical structure which favores mist-nets effectiveness (Fig. 1d).

Yearly patterns of abundance of resident and migratory birds show variations within year and across land use types (Fig. 5a, c), however mean abundance remains stable across years within land uses except for the resident community in the TEPL, MACO and SICO (Fig. 5a) land uses. Mean resident abundance yearly patterns in these land uses follows the same trends observed for overall bird abundance (Fig. 4a), which indicates the overall trends are determined by changes in the resident community as the migratory community remains stable across years and land uses. Monthly patterns of abundance in the resident community show decreases in bird captures from june to december in all land use types (Fig. 5b). Furthermore, monthly patterns of migratory bird abundance coincides with patterns observed for overall species richness (Fig. 2b) with a clear drop in number of individuals during the April-September period (Fig. 5d) which corresponds to migration season.

Bird community similarities across years and land use types

Our General Procrustes Analysis (GPA) showed similarities in bird communities within land uses across years (Fig. 6). We ran a first GPA as to group land uses that have been monitored during the 2008-2014 period. Results from this first analysis show that our agroforest land uses MACA, MACO and SICO have had similar bird composition throughout the seven years of sampling with year to year changes but no clear direction of change (Fig. 6a). MACO and MACA which are the most vertically complex agroforests were also the land

uses more similar in bird species composition compared to the FORE land use. Bird species commonly shared between these agroforests include Chestnut-sided Warbler *Setophaga pensylvanica*, White-collared Manakin *Manacus candei*, and House Wren *Troglodytes aedon* (Fig. S5-S8). Additionally, at the other end of the intensification gradient our land uses LIFE and SUCA were more similar between them than with the rest of the agricultural land uses. The bird community present in LIFE and SUCA showed very little change between years, resulting in more stationary communities. These less forested land uses shared species typical of open areas such as the Blue-black Grassquit *Volatinia jacarina*, Gray-crowned Yellowthroat *Geothlypis poliocephala* and Variable Seedeater *Sporophila corvina*. Finally, our FORE land use showed a stationary and unique bird community when compared to the agricultural land uses. Species associated to FORE include White-breasted Wood-Wren *Henicorhina leucosticta*, Ochre-bellied Flycatcher *Mionectes oleagineus*, Long-billed Hermit *Phaethornis longirostris* and Stripe-throated Hermit *Phaethornis striigularis*.

Our second GPA including our TEPL and MSPL land uses showed similar trends. Bird communities in TEPL and MSPL are very similar to our MACA and SICO land uses (Fig. 6b). Changes in bird species composition between our agroforest land uses and forest plantations for the years 2012-2014, showed a circular directionality for most land uses with the exception of SICO. Similarities and dissimilarities described previously remained for the rest of land uses, with our simplified systems LIFE and SUCA been very similar between them and our FORE land use being the most dissimilar when compared to the rest of land uses (Fig. 6a, b; Fig. S5-S8). Overall, our MACA, MACO, SICO, TEPL and MSPL showed the greatest beta diversity (Fig. 6a, b; Fig. S5-S8).

Discussion

Using captured data from long-term mist-netting stations we found that the majority of sampling units across land uses within the Volcanica Central Talamanca Biological Corridor (VCTBC) are capable of supporting stable bird communities. Stability understood as no changes from year to year in mean species richness and abundance (Jarvinen 1979, Boulinier *et al.* 1998, Karp *et al.* 2011), of either the total population, or of resident and migratory species over a seven-year period (Fig. 2 and Fig. 4).

Only two out of the eight sampling units within land uses showed indication of change in overall mean species richness and abundance. Our MACO land use showed an annual decreasing trend in overall species richness and abundance (Fig. 2a and Fig. 4a) which was the result of these trends been predominant within the resident community while absent in the migratory community (Fig. 3a-c, Fig. 5a-c). Annual declines in mean species richness might be the result of a drastic net avoidance reaction (MacArthur and MacArthur 1974) from some resident species within this land use having also impacts on bird abundance (Marques *et al.* 2013). Resident birds captured in the MACO land use represented in the first and second year 73% and 69% of all captures respectively (Table 1), with many species captured only during the first year (2008) or during the first and second year (2008-2009) of sampling while remaining absent in following years. Resident species captured only during the first two years of sampling includes the Passerini's Tanager *Ramphocelus passerinii*, a species associated to non forested areas (Stiles 1985) usually observed at low elevations in gardens and open areas (Garrigues and Dean 2014), from which captured numbers varied from twelve to five individuals in the first and second year respectively evidencing the implications for the mean bird abundance metric. Absence of these species is revealed in the bird composition analysis

of the MACO land use, which showed that bird community for the years 2008 and 2009 was more distinct than in following years (Fig. 6a), also indicating as found in other studies (Marques *et al.* 2013) that common captured species do not show signs of net avoidance as community composition remained very similar in following years. Furthermore, mean species richness and abundance decreasing patterns were unique to the MACO land use which was also subject to management interventions in October 2010, when trees were harvested and half the original land use area was converted into TEPL. This intervention created a "gap" adjacent to the remaining MACO which has progressively been growing with some community composition recovery which suggests adjacent land uses might be playing an important role at compensating potential negative effects derive from on-site interventions (Devictor and Jiguet 2007), as the MACO land use is adjacent to a well preserved forest strip that connects these agroforests areas with our FORE land use.

The SICO land use showed a slight increase in overall mean species richness and abundance which was the result of particularly high resident species capture rates during the years 2011, 2012 and parts of 2013 (Fig. S2b). This high capture rate might have been influenced by site management interventions in those years, as poró trees at the SICO land use are pruned twice a year to boost coffee growth (Beer *et al.* 1998), potentially allowing this management practice to produce a short-term effect on food resource availability favoring bird captures, as pruning has been shown to affect arboreal arthropod communities (Philpott 2005). For example, Johnson (2000) found that arthropod communities in shade trees within coffee plantations were up to four times more abundant in the canopy than in the understory which could increase arthropod availability after a pruning event, however, more information is needed to back this hypothesis especially due to the multiple tradeoffs related to shade

management activities (Tscharntke *et al.* 2011). Additionally, vertical structure in the SICO land use (Fig. 1d) may have allowed a more effective capture of dispersal events compared to our other more vertically complex land uses due to biases in mistnetting protocols (Dunn and Ralph 2004). Overlapping of mist netting sampling during dispersal events could have boost captures affecting the mean species and abundance metrics on those particular years.

Metrics of mean migratory species richness and abundance showed stability of the migratory community across years and land uses (Fig. 3c, d; Fig. 5c, d). The only predominant pattern within the migratory community was the one associated with annual migratory events in which mean migratory species richness and abundance plummets affecting overall species richness metrics across land uses.

Avian community stability within our different land uses is a reflection of the overall landscape stability. Brenes (2009) showed through a multi-temporal landuse change analysis of the VCTBC that forest cover have remained stable for the last 22 years with an average of 39.5%. Estrada (2009), on the other hand, constructed functional connectivity scenarios for three bird species with different degrees of forest dependency and found that the VCTBC landscape provides 85% functional habitat patches for Passerini's Tanager *Ramphocelus passerinii*, 40% for Chestnut-sided Warbler *Setophaga pensylvanica* and 37% for Ochre-bellied Flycatcher *Mionectes oleagineus*, being the latter the species with the greatest forest dependency. These results indicate this landscape is connected in different degrees depending on forest dependency of the species, suggesting that the VCTBC allows species mobility and thus maintenance of population dynamic processes essential for the survival of these populations in human-modified landscapes (Hanski and Ovaskainen 2003). Additionally, Devictor and Jiguet (2007) found that more homogeneous landscapes providing low species

connectivity causes increases in community instability suggesting that the presence of more diverse surrounding habitats support the maintenance of stable communities. Forest cover stability in this landscape as in other regions in Costa Rica is the result of Forestry Law 7575, approved in 1996, which forbids conversion of forested areas and which have contributed to halting national scale deforestation (Robalino and Pfaff 2013) and to maintain forest cover within the VCTBC.

Our results provide additional evidence on the importance of forest fragments remaining in human-modified landscapes for biodiversity conservation. Our forest site (FORE) supported a unique bird community when compared to other agricultural land use types (Fig. 6a, b), these results agreed with findings by Petit and Petit (2003) who also highlighted the importance of shaded coffee plantations for vulnerable bird species. Our findings indicate that agroforestry systems such as multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA) and simplified coffee agroforest (SICO) shared many species with our FORE land use, supporting the contention that agroforestry systems are an important alternative to balance production and conservation (Tscharntke *et al.* 2011, Hernandez *et al.* 2013, Buechley *et al.* 2015, McDermott *et al.* 2015). Our simplest land use types in terms of vertical structure included live fences (LIFE) and sugar cane (SUCA), and these supported bird species typical of open areas. However, our LIFE land use also supported species with certain degree of forest dependence which supports the notion that live fences are important elements within agricultural landscapes as they provide structural connectivity and food resources for a diversity of animal species (Harvey *et al.* 2005). Finally, our results also provide further evidence on the land-use cascade effect as composition of bird communities changed as we moved in a gradient of management intensification highlighting the

importance of forest fragments remaining in agricultural landscapes for the persistence of bird species of conservation concern.

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Data availability statement

Data will be made publicly available prior to publication.

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Figures

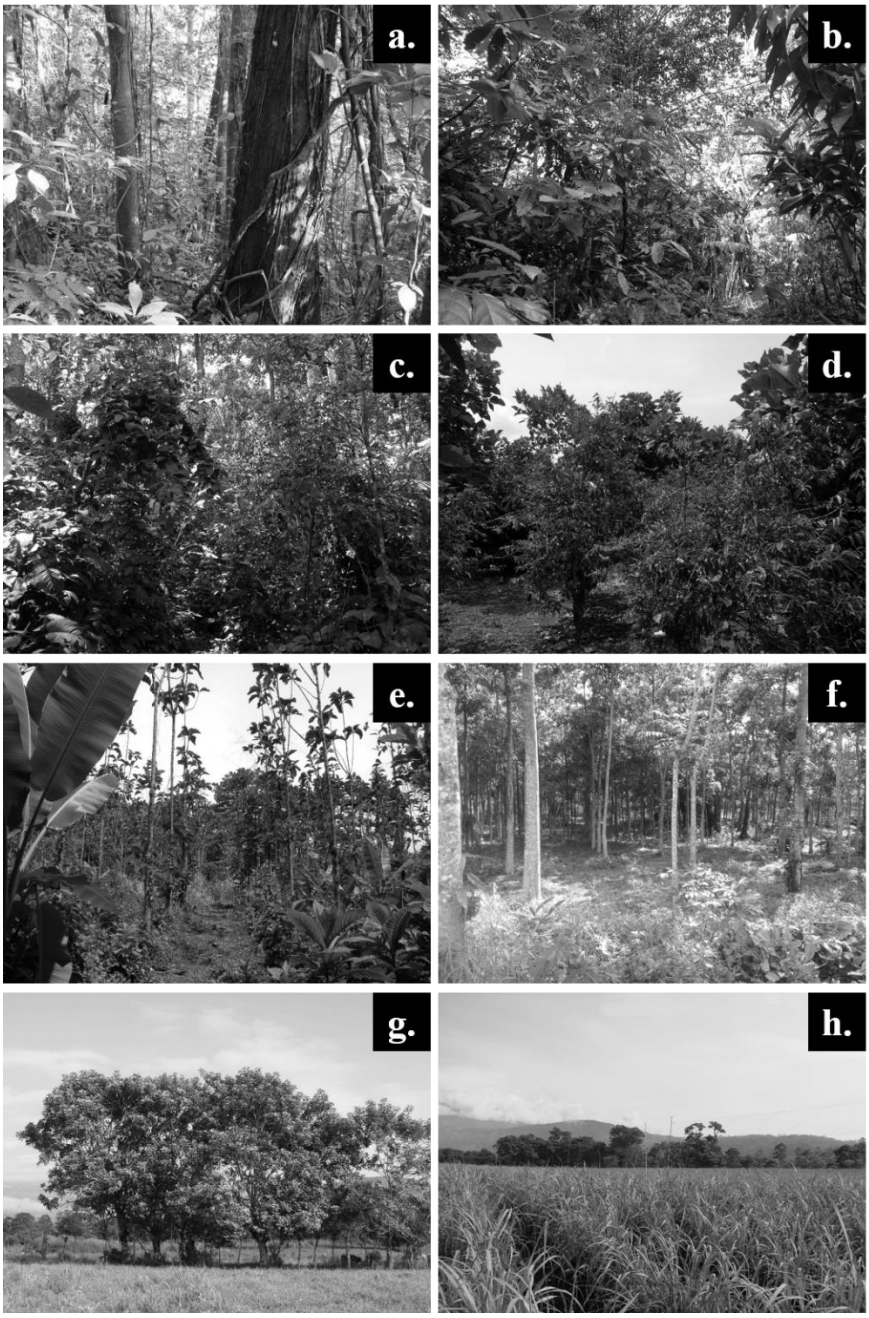

Figure 1. Different land use types under monitoring. (a) secondary mature forest (FORE), (b) multi strata cacao agroforest (MACA), (c) multi strata coffee agroforest (MACO), (d) simplified coffee agroforest (SICO), (e) teak plantation (TEPL), (f) mixed species plantation (MSPL), (g) pastures with live fences (LIFE), and (h) sugar cane (SUCA).

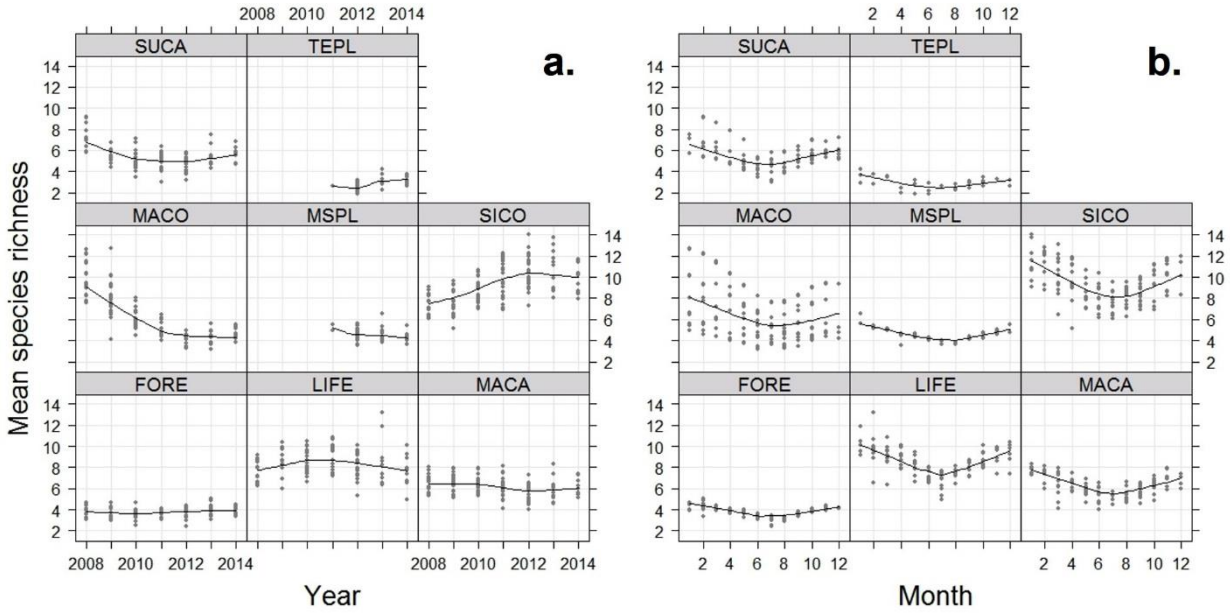

Figure 2. Yearly and monthly patterns of total population bird species richness predicted values. Where sugar cane (SUCA), teak plantation (TEPL), multi strata coffee agroforest (MACO), mixed species plantation (MSPL), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA).

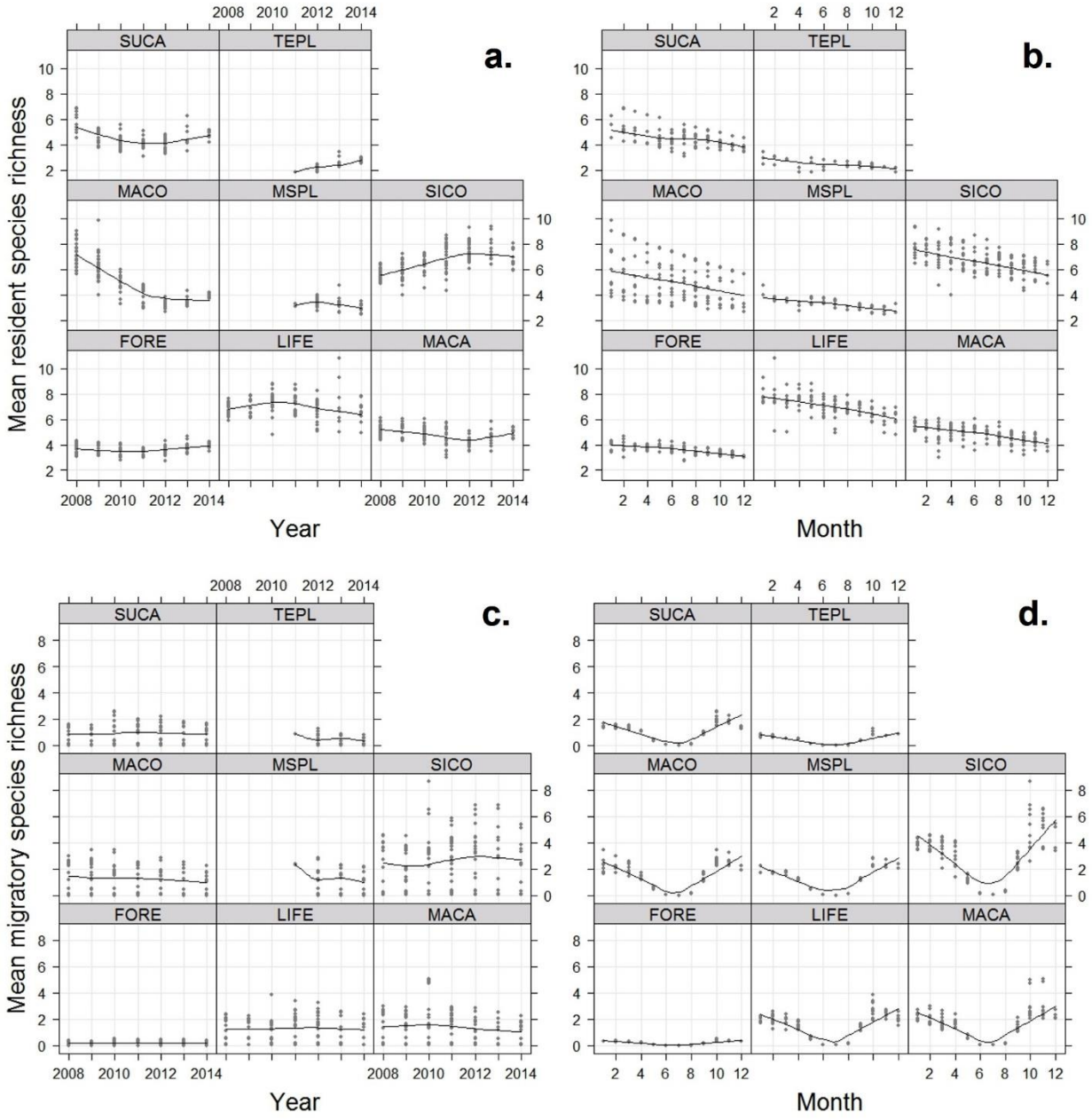

Figure 3. Yearly and monthly patterns of resident (a-b) and migratory (c-d) species richness predicted values. Where sugar cane (SUCA), teak plantation (TEPL), multi strata coffee agroforest (MACO), mixed species plantation (MSPL), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA).

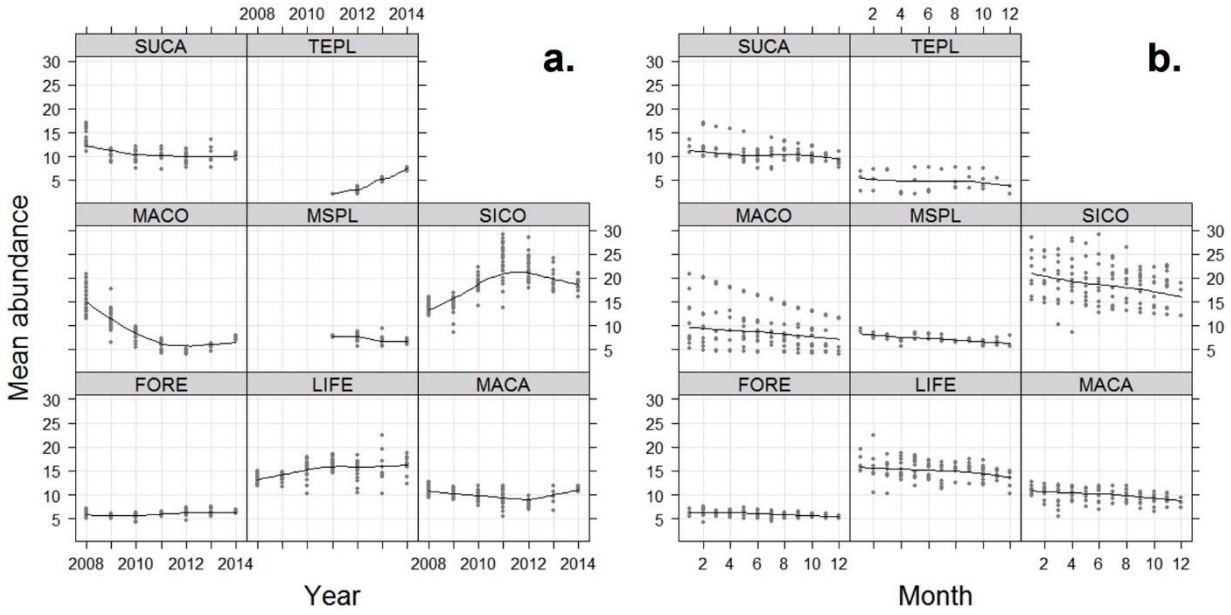

Figure 4. Yearly and monthly patterns of bird abundance predicted values. Where sugar cane (SUCA), teak plantation (TEPL), multi strata coffee agroforest (MACO), mixed species plantation (MSPL), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA).

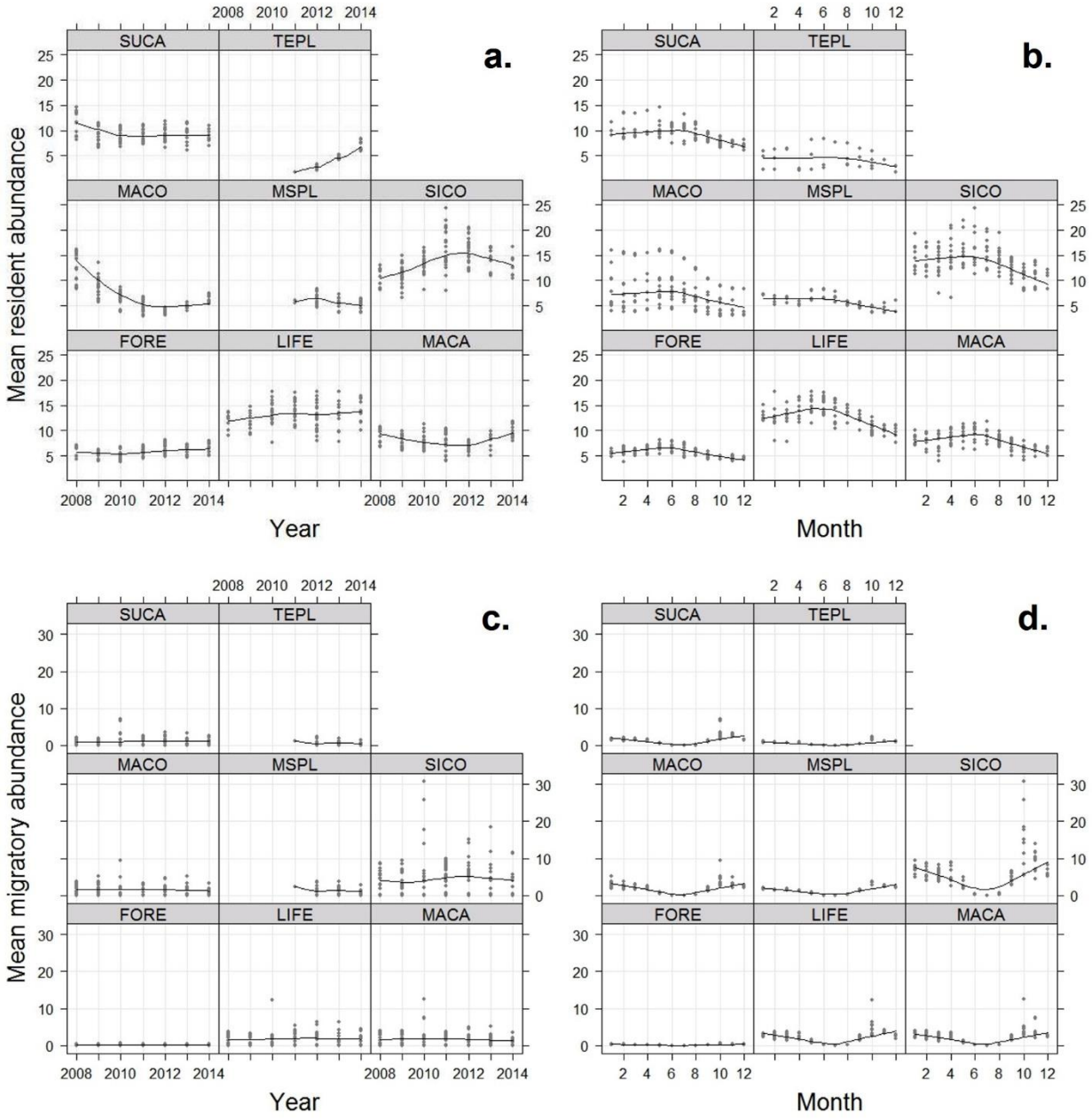

Figure 5. Yearly and monthly patterns of mean resident (a-b) and mean migratory (c-d) abundance predicted values. Where sugar cane (SUCA), teak plantation (TEPL), multi strata coffee agroforest (MACO), mixed species plantation (MSPL), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA).

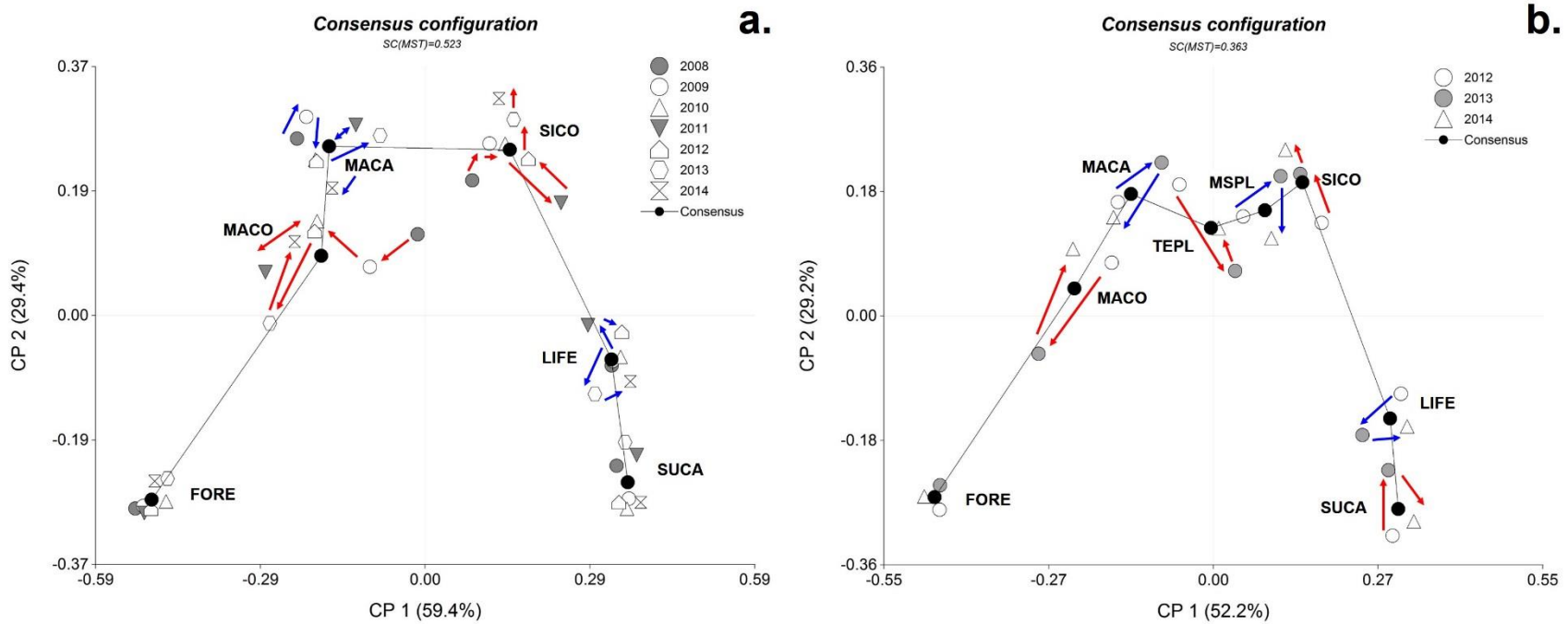

Figure 6. Generalised Procrustes Analysis (GPA) showing bird community consensus per land use. (a) Consensus for the years 2008-2014, (b) consensus for the years 2012-2014 where secondary mature forest (FORE), multi strata coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE), sugar cane (SUCA), teak plantation (TEPL) and mixed species plantation (MSPL). Arrows show direction of change of the bird community composition throughout the years. Lines connecting different land uses correspond to the minimum spanning tree (MST). Land uses connected by the MST that are closer are more similar between them than those farther apart (i.e. FORE and SUCA being the most dissimilar of all land uses).

Table 1. Total resident (R) and migratory (M) birds captured by land use between the years 2008 to 2014. Land uses correspond to forest (FORE), multi-strata agroforestry coffee (MACO), sugar cane (SUCA), multi-strata agroforestry cacao (MACA), simplified coffee agroforest (SICO), live fences (LIFE), mixed species plantation (MSPL), and teak plantation (TEPL). "Abu" is an abbreviation for abundance, total sampling corresponds to the number of days sampled and net effort corresponds to the total number of hours mist-nets remained opened.

Station	2008		2009		2010		2011		2012		2013		2014		Total		Abu	%
	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M		
FORE	127	2	56	0	75	6	94	4	117	1	62	1	72	1	603	15	618	7.06
MACO	349	74	186	50	139	27	104	20	57	13	49	12	68	13	952	209	1161	13.27
MACA	187	32	148	46	178	55	122	34	134	40	77	22	103	12	949	241	1190	13.60
SICO	292	63	220	64	276	169	431	157	357	138	151	51	148	58	1875	700	2575	29.43
TEPL							2	0	29	7	35	3	79	7	145	17	162	1.85
MSPL							25	4	116	24	53	9	50	18	244	55	299	3.42
LIFE	255	22	147	26	267	41	228	32	303	53	117	39	161	13	1478	226	1704	19.47
SUCA	181	34	90	11	153	13	156	18	204	15	69	8	78	11	931	110	1041	11.90
Abu	1391	227	847	197	1088	311	1162	269	1317	291	613	145	759	133	7177	1573	8750	
Total Sampling dates		124		105		109		114		156		80		81		769		
Net effort (net hours)		3289		2787		2758		2831		3625		2178		1978		19,446		

Table 2. Ten most common bird species captured across land uses between the years 2008 to 2014. Status refers to whether the species are considered all year residents (R) or Neotropical migrants (NM); S refers to the status classification and follows the "Official List of the Birds of Costa Rica", annually updated and published by the Costa Rican Ornithological Association (AOCR).

Family	Latin Name	English Name	S	Abu.	%
Trochilidae	*Amazilia tzacatl*	Rufous-tailed Hummingbird	R	1198	13.69
Thraupidae	*Sporophila corvina*	Variable Seedeater	R	938	10.72
Thraupidae	*Volatinia jacarina*	Blue-black Grassquit	R	848	9.69
Thraupidae	*Tiaris olivaceus*	Yellow-faced Grassquit	R	460	5.26
Tyrannidae	*Mionectes oleagineus*	Ochre-bellied Flycatcher	R	398	4.55
Trochilidae	*Phaethornis striigularis*	Stripe-throated Hermit	R	282	3.22
Parulidae	*Setophaga pensylvanica*	Chestnut-sided Warbler	NM	225	2.57
Parulidae	*Setophaga petechia*	Yellow Warbler	NM	198	2.26
Troglodytidae	*Troglodytes aedon*	House Wren	R	180	2.06
Parulidae	*Geothlypis philadelphia*	Mourning Warbler	R	178	2.03

Table 3. Variable significance at predicting overall species richness (SR) and abundance (AB) as well as resident and migratory SR and AB. Where different land use types (land use); sampling dates converted to a continuous numerical value (Time); sampling effort measured as the total number of hours mist-nets remained open at each sampling event at each land use type (effort); and calendar month at which land use types were sampled (month). The ":" symbol denotes interaction. Variables significance was assessed via GAMM models (n = 769).

Response variable	Family	R-adj.	Deviance explained	Predictor variables	χ^2	P
Species richness	Negative binomial	0.394	40.5%	Land use	4.462	< **0.0001**
				Time:Land use	3421.311	0.5900
				Month	59.371	< **0.0001**
				Effort	25.371	< **0.0001**
Abundance	Negative binomial	0.317	37.4%	Land use	2.607	< **0.0001**
				Time:Land use	4657.098	0.5144
				Month	6.602	**0.0103**
				Effort	19.567	< **0.0001**
Resident species richness	Negative binomial	0.314	32.1%	Land use	4.114	< **0.0001**
				Time:Land use	1446.283	0.6630
				Month	22.864	< **0.0001**
				Effort	27.453	< **0.0001**
Resident abundance	Negative binomial	0.294	33.9%	Land use	2.174	< **0.0001**
				Time:Land use	2329.060	0.6060
				Month	39.156	< **0.0001**
				Effort	21.169	< **0.0001**
Migratory species richness	Zero inflated Poisson		45.9%	Land use	90.35	< **0.0001**
				Time:Month	22.82	**0.0004**
				Effort	25.90	< **0.0001**
Migratory abundance	Zero inflated Poisson		51.8%	Land use	291.30	< **0.0001**
				Time:Month	174.43	< **0.0001**
				Effort	26.13	< **0.0001**

Supplementary Information

Table S1. List of bird species captured on a forest site and seven agricultural land uses during the years 2008 to 2014. S-Status, R-Residents, M-Migratory.

Family	S	Code	Latin Name	English Name
Cracidae				
	R	ORTCIN	*Ortalis cinereiceps*	Gray-headed Chachalaca
Accipitridae				
	R	RUPMAG	*Rupornis magnirostris*	Roadside Hawk
Rallidae				
	R	LATALB	*Laterallus albigularis*	White-throated Crake
Columbidae				
	R	PATFLA	*Patagioenas flavirostris*	Red-billed Pigeon
	R	COLINC	*Columbina inca*	Inca Dove
	R	COLPAS	*Columbina passerina*	Common Ground-Dove
	R	COLMIN	*Columbina minuta*	Plain-breasted Ground-Dove
	R	COLTAL	*Columbina talpacoti*	Ruddy Ground-Dove
	R	CLAPRE	*Claravis pretiosa*	Blue Ground-Dove
	R	GEOMON	*Geotrygon montana*	Ruddy Quail-Dove
	R	LEPVER	*Leptotila verreauxi*	White-tipped Dove
	R	LEPCAS	*Leptotila cassinii*	Gray-Chested Dove
Cuculidae				
	M	COCMIR	*Coccyzus minor*	Mangrove Cuckoo
	R	CROSUL	*Crotophaga sulcirostris*	Groove-billed Ani
Caprimulgidae				
	R	ANTRUF	*Antrostomus rufus*	Rufous Nightjar
	M	ANTVOC	*Antrostomus vociferus*	Eastern Whip-poor-will
	R	NYCALB	*Nyctidromus albicollis*	Common Pauraque
Trochilidae				
	R	AMAAMB	*Amazilia amabilis*	Blue-chested Hummingbird
	R	AMACYR	*Amazilia cyanura*	Blue-tailed Hummingbird
	R	AMASAU	*Amazilia saucerrottei*	Steely-vented Hummingbird
	R	AMATZA	*Amazilia tzacatl*	Rufous-tailed Hummingbird
	R	ANTPRE	*Anthracothorax prevostii*	Green-breasted Mango
	R	CAMHEM	*Campylopterus hemileucurus*	Violet Sabrewing
	R	CHAURO	*Chalybura urochrysia*	Bronze-tailed Plumeleteer
	R	COLDEL	*Colibri delphinae*	Brown Violetear
	R	EUGFUL	*Eugenes fulgens*	Magnificent Hummingbird

Family	S	Code	Latin Name	English Name
Trochilidae				
	R	FLOMEL	*Florisuga mellivora*	White-necked Jacobin
	R	HELLON	*Heliomaster longirostris*	Long-billed Starthroat
	R	HYLELI	*Hylocharis eliciae*	Blue-throated Goldentail
	R	PHAGUY	*Phaethornis guy*	Green Hermit
	R	PHALON	*Phaethornis longirotris*	Long-billed Hermit
	R	PHASTR	*Phaethornis striigularis*	Stripe-throated Hermit
	R	THACOL	*Thalurania colombica*	Crowned Woodnymph
	R	THRRUC	*Threnetes ruckeri*	Band-tailed Barbthroat
Trogonidae				
	R	TROCAL	*Trogon caligatus*	Gartered Trogon
	R	TRORUS	*Trogon rufus*	Black-throated Trogon
Momotidae				
	R	BARMAR	*Baryphthengus martii*	Rufous Motmot
	R	MOMMOM	*Momotus momota*	Blue-crowned Motmot
Ramphastidae				
	R	PTETOR	*Pteroglossus torquatus*	Collared Aracari
	R	RAMSUL	*Ramphastos sulfuratus*	Keel-billed Toucan
Picidae				
	R	MELHOF	*Melanerpes hoffmannii*	Hoffmann´s Woodpecker
	R	PICSIM	*Piculus simplex*	Rufous-winged Woodpecker
Psittacidae				
	R	AMAALB	*Amazona albifrons*	White-fronted Parrot
	R	PIOSEN	*Pionus senilis*	White-crowned Parrot
Thamnophilidae				
	R	CERTYR	*Cercomacra tyrannina*	Dusky Antbird
	R	EPIFUL	*Epinecrophylla fulviventris*	Checker-throated Antwren
	R	MYREXS	*Myrmeciza exsul*	Chestnut-backed Antbird
	R	TARMAJ	*Taraba major*	Great Antshrike
	R	THAATR	*Thamnophilus atrinucha*	Black-crowned Antshrike
	R	THADOL	*Thamnophilus doliatus*	Barred Antshrike
Furnariidae				
	R	AUTOCH	*Automolus ochrolaemus*	Buff-throated Foliage-gleaner
	R	DECLON	*Deconychura longicauda*	Long-tailed Woodcreeper
	R	DECFUL	*Dendrocincla fuliginosa*	Plain-brown Woodcreeper
	R	DENPIC	*Dendrocolaptes picumnus*	Black-banded Woodcreeper

Family	S	Code	Latin Name	English Name
Furnariidae				
	R	DENSAN	*Dendrocolaptes sanctithomae*	Northern-barred Woodcreeper
	R	LEPAFF	*Lepidocolaptes affinis*	Spot-crowned Woodcreeper
	R	LEPSOU	*Lepidocolaptes souleyetii*	Streak-headed Woodcreeper
	R	SYNBRA	*Synallaxis brachyura*	Slaty Spinetail
	R	XENMIT	*Xenops minutus*	Plain Xenops
	R	XIPERY	*Xiphorhynchus erythropygius*	Spotted Woodcreeper
	R	XIPSUS	*Xiphorhynchus susurrans*	Cocoa Woodcreeper
Tyrannidae				
	R	APHCAP	*Aphanotriccus capitalis*	Tawny-chested Flycatcher
	R	ATTSPA	*Attila spadiceus*	Bright-rumped Attila
	R	CAMIMB	*Camptostoma imberbe*	Northern Beardless-Tyrannulet
	R	CAPFLA	*Capsiempis flaveola*	Yellow Tyrannulet
	R	CONCIN	*Contopus cinereus*	Tropical Pewee
	M	CONSOR	*Contopus sordidulus*	Western Wood-Pewee
	M	CONVIR	*Contopus virens*	Eastern Wood-Pewee
	R	ELAFLA	*Elaenia flavogaster*	Yellow-bellied Elaenia
	R	ELAFRA	*Elaenia frantzii*	Mountain Elaenia
	R	EMPALB	*Empidonax albigularis*	White-throated Flycatcher
	M	EMPALN	*Empidonax alnorum*	Alder Flycatcher
	R	EMPATR	*Empidonax atriceps*	Black-capped Flycatcher
	R	EMPFLS	*Empidonax flavescens*	Yellowish Flycatcher
	M	EMPFLN	*Empidonax flaviventris*	Yellow-bellied Flycatcher
	M	EMPMIN	*Empidonax minimus*	Least Flycatcher
	M	EMPVIR	*Empidonax virescens*	Acadian Flycatcher
	R	LEGLEU	*Legatus leucophaius*	Piratic Flycatcher
	R	LEPSUP	*Leptopogon superciliaris*	Slaty-capped Flycatcher
	R	MIOOLE	*Mionectes oleagineus*	Ochre-bellied Flycatcher
	M	MYICIN	*Myiarchus cinerascens*	Ash-throated Flycatcher
	M	MYICRI	*Myiarchus crinitus*	Great Crested Flycatcher
	R	MYITUB	*Myiarchus tuberculifer*	Dusky-capped Flycatcher
	R	MYILUT	*Myiodynastes luteiventris*	Sulphur-bellied Flycatcher
	R	MYOGRA	*Myiozetetes granadensis*	Gray-capped Flycatcher
	R	MYISIM	*Myiozetetes similis*	Social Flycatcher
	R	ONCCIN	*Oncostoma cinereigulare*	Northern Bentbill
	R	PITSUL	*Pitangus sulphuratus*	Great Kiskadee

Family	S	Code	Latin Name	English Name
Tyrannidae				
	R	SAYNIG	*Sayornis nigricans*	Black Phoebe
	R	TERERY	*Terenotriccus erythrurus*	Ruddy-tailed Flycatcher
	R	TODCIN	*Todirostrum cinereum*	Common Tody-Flycatcher
	R	TOLASS	*Tolmomyias assimilis*	Yellow-margined Flycatcher
	R	TOLSUL	*Tolmomyias sulphurescens*	Yellow-olive Flycatcher
	R	TYRMEL	*Tyrannus melancholicus*	Tropical Kingbird
	R	ZIMVIL	*Zimmerius vilissimus*	Paltry Tyrannulet
Tytiridae				
	R	PACCIN	*Pachyramphus cinnamomeus*	Cinnamon Becard
	R	PACPOL	*Pachyramphus polychopterus*	White-winged Becard
Pipridae				
	R	CORALT	*Corapipo altera*	White-ruffed Manakin
	R	MANCAN	*Manacus candei*	White-collared Manakin
Vireonidae				
	R	HYLDEC	*Hylophilus decurtatus*	Lesser Greenlet
	R	HYLOCH	*Hylophilus ochraceiceps*	Tawny-crowned Greenlet
	M	VIRFLF	*Vireo flavifrons*	Yellow-throated Vireo
	R	VIRFLD	*Vireo flavoviridis*	Yellow-green Vireo
	M	VIRGRI	*Vireo griseus*	White-eyed Vireo
	M	VIROLI	*Vireo olivaceus*	Red-eyed Vireo
	M	VIRPHI	*Vireo philadelphicus*	Philadelphia Vireo
Corvidae				
	R	PSIMOR	*Psilorhinus morio*	Brown Jay
Hirundinidae				
	M	HIRRUS	*Hirundo rustica*	Barn Swallow
	M	PETPYR	*Petrochelidon pyrrhonota*	Cliff Swallow
	M	PIGCYA	*Pygochelidon cyanoleuca*	Blue-and-white Swallow
	M	RIPRIP	*Riparia riparia*	Bank Swallow
	R	STERUF	*Stelgidopteryx ruficollis*	Southern Rough-winged Swallow
	R	STESER	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow
Troglodytidae				
	R	CANMOD	*Cantorchilus modestus*	Plain Wren
	R	CANNIG	*Cantorchilus nigricapillus*	Bay Wren
	R	CANTHO	*Cantorchilus thoracicus*	Stripe-breasted Wren

Family	S	Code	Latin Name	English Name
Troglodytidae				
	R	HENLES	*Henicorhina leucosticta*	White-breasted Wood-Wren
	R	MICMAR	*Microcerculus marginatus*	Scaly-breasted Wren
	R	MICPHI	*Microcerculus philomela*	Nightingale Wren
	R	PHEATR	*Pheugopedius atrogularis*	Black-throated Wren
	R	THRPLE	*Thryophilus pleurostictus*	Banded Wren
	R	THRRUL	*Thryophilus rufalbus*	Rufous-and-white Wren
	R	TROAED	*Troglodytes aedon*	House Wren
Polioptilidae				
	R	POLPLU	*Polioptila plumbea*	Tropical Gnatcatcher
	R	RAMMEL	*Ramphocaenus melanurus*	Long-billed Gnatwren
Turdidae				
	R	CATAUN	*Catharus aurantiirostris*	Orange-billed Nightingale-Thrush
	M	CATFUS	*Catharus fuscescens*	Veery
	M	CATMIN	*Catharus minimus*	Gray-cheeked Thrush
	M	CATUST	*Catharus ustulatus*	Swainson’s Thrush
	M	HYLMUS	*Hylocichla mustelina*	Wood Thrush
	R	TURASS	*Turdus assimilis*	White-throated Thrush
	R	TURGRA	*Turdus grayi*	Clay-colored Thrush
Mimidae				
	M	DUMCAR	*Dumetella carolinensis*	Gray Catbird
Parulidae				
	R	BASRUF	*Basileuterus rufifrons*	Rufous-capped Warbler
	M	CARCAN	*Cardellina canadensis*	Canada Warbler
	M	CARPUS	*Cardellina pusilla*	Wilson´s Warbler
	M	GEOFOR	*Geothlypis formosa*	Kentucky Warbler
	M	GEOPHI	*Geothlypis philadelphia*	Mourning Warbler
	R	GEOPOL	*Geothlypis poliocephala*	Gray-crowned Yellowthroat
	R	GEOSEM	*Geothlypis semiflava*	Olive-crowned Yellowthroat
	M	GEOTOL	*Geothlypis tolmiei*	MacGillivray's Warbler
	M	GEOTRI	*Geothlypis trichas*	Common Yellowthroat
	M	HELVER	*Helmitheros vermivorum*	Worm-eating Warbler
	M	ICTVIR	*Icteria virens*	Yellow-breasted Chat
	M	MNIVAR	*Mniotilta varia*	Black-and-white Warbler
	M	OREPER	*Oreothlypis peregrina*	Tennessee Warbler
	M	PARNOV	*Parkesia noveboracensis*	Northern Waterthrush

Family	S	Code	Latin Name	English Name
Parulidae				
	M	PROCIT	*Protonotaria citrea*	Prothonotary Warbler
	M	SEIAUR	*Seiurus aurocapilla*	Ovenbird
	M	SETCAS	*Setophaga castanea*	Bay-breasted Wren
	M	SETCIT	*Setophaga citrina*	Hooded Warbler
	M	SETFUS	*Setophaga fusca*	Blackburnian Warbler
	M	SETMAG	*Setophaga magnolia*	Magnolia Warbler
	M	SETPEN	*Setophaga pensylvanica*	Chestnut-sided Warbler
	M	SETPET	*Setophaga petechia*	Yellow Warbler
	R	SETPIT	*Setophaga pitiayumi*	Tropical Parula
	M	SETRUT	*Setophaga ruticilla*	American Redstart
	M	SETSTR	*Setophaga striata*	Blackpoll Warbler
	M	SETVIR	*Setophaga virens*	Black-throated Green Warbler
	M	VERCHR	*Vermivora chrysoptera*	Golden-winged Warbler
	M	VERCYA	*Vermivora cyanoptera*	Blue-winged Warbler
Thraupidae				
	R	DACVEN	*Dacnis venusta*	Scarlet-thighed Dacnis
	R	RAMPAS	*Ramphocelus passerinii*	Passerini's Tanager
	R	TACDEL	*Tachyphonus delattrii*	Tawny-crested Tanager
	R	TACLUC	*Tachyphonus luctuosus*	White-shouldered Tanager
	R	TACRUF	*Tachyphonus rufus*	White-lined Tanager
	R	TANLAR	*Tangara larvata*	Golden-hooded Tanager
	R	THREPI	*Thraupis episcopus*	Blue-gray Tanager
	R	THRPAL	*Thraupis palmarum*	Palm Tanager
	R	COEFLA	*Coereba flaveola*	Bananaquit
	R	TIAOLI	*Tiaris olivaceus*	Yellow-faced Grassquit
	R	VOLJAC	*Volatinia jacarina*	Blue-black Grassquit
	R	SPOCOR	*Sporophila corvina*	Variable Seedeater
	R	SPOFUN	*Sporophila funerea*	Thick-billed Seed-Finch
	R	SPONIG	*Sporophila nigricollis*	Yellow-Bellied Seedeater
	R	SPONUT	*Sporophila nuttingi*	Nicaraguan Seed-Finch
	R	SPOTOR	*Sporophila torqueola*	White-collared Seedeater
	R	SALATR	*Saltator atriceps*	Black-headed Saltator
	R	SALCOE	*Saltator coerulescens*	Grayish Saltator
	R	SALMAX	*Saltator maximus*	Buff-throated Saltator

Family	S	Code	LatinName	EnglishName
Emberizidae				
	R	ARRAUR	*Arremon aurantiirostris*	Orange-billed Sparrow
	R	ARRCON	*Arremonops conirostris*	Black-striped Sparrow
	R	MELBIA	*Melozone biarcuata*	Prevost´s Ground-Sparrow
	R	ZONTRI	*Zonotrichia capensis*	Rufous-collared Sparrow
Cardinalidae				
	R	CHLCAR	*Chlorothraupis carmioli*	Carmiol's Tanager
	R	CYACYD	*Cyanocompsa cyanoides*	Blue-black Grosbeak
	R	HABFUS	*Habia fuscicauda*	Red-throated Ant-tanager
	R	PASCAE	*Passerina caerulea*	Blue Grosbeak
	M	PASCIR	*Passerina ciris*	Painted Bunting
	M	PASCYA	*Passerina cyanea*	Indigo Bunting
	M	PHELUD	*Pheucticus ludovicianus*	Rose-breasted Grosbeak
	M	PIROLI	*Piranga olivacea*	Scarlet Tanager
	M	PIRRUB	*Piranga rubra*	Summer Tanager
Icteridae				
	R	AMBHOL	*Amblycercus holosericeus*	Yellow-billed Cacique
	M	ICTGAL	*Icterus galbula*	Baltimore Oriole
	M	ICTSPU	*Icterus spurius*	Orchard Oriole
	R	MOLAEN	*Molothrus aeneus*	Bronzed Cowbird
	R	PSAMON	*Psarocolius montezuma*	Montezuma Oropendola
	R	QUIMEX	*Quiscalus mexicanus*	Great-tailed Grackle
	R	STUMAG	*Sturnella magna*	Eastern Meadowlark
Fringillidae				
	R	EUPGOU	*Euphonia gouldi*	Olive-backed Euphonia
	R	EUPHIR	*Euphonia hirundinacea*	Yellow-throated Euphonia
	R	EUPIMI	*Euphonia imitans*	Spot-crowned Euphonia
	R	EUPLAN	*Euphonia laniirostris*	Thick-billed Euphonia
	R	EUPLUT	*Euphonia luteicapilla*	Yellow-crowned Euphonia
	R	EUPMIN	*Euphonia minuta*	White-vented Euphonia

Table S2a. Results from the Generalised Procrustes Analysis (GPA) for the years 2008 to 2014 where secondary mature forest (FORE), multi strata agroforestry coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), live fences (LIFE) and sugar cane (SUCA).

Land use	**Proportion consensus**
FORE	0.993
MACO	0.856
MACA	0.901
SICO	0.917
LIFE	0.947
SUCA	0.971
Total	0.949

Table S2b. Results from the Generalised Procrustes Analysis (GPA) for the years 2012 to 2014 where secondary mature forest (FORE), multi strata agroforestry coffee agroforest (MACO), multi strata cacao agroforest (MACA), simplified coffee agroforest (SICO), mixed species plantation (MSPL), teak plantation (TEPL), live fences (LIFE) and sugar cane (SUCA).

Land use	**Proportion consensus**
FORE	0.995
MACO	0.818
MACA	0.911
SICO	0.976
TEPL	0.858
MSPL	0.935
LIFE	0.961
SUCA	0.974
Total	0.953

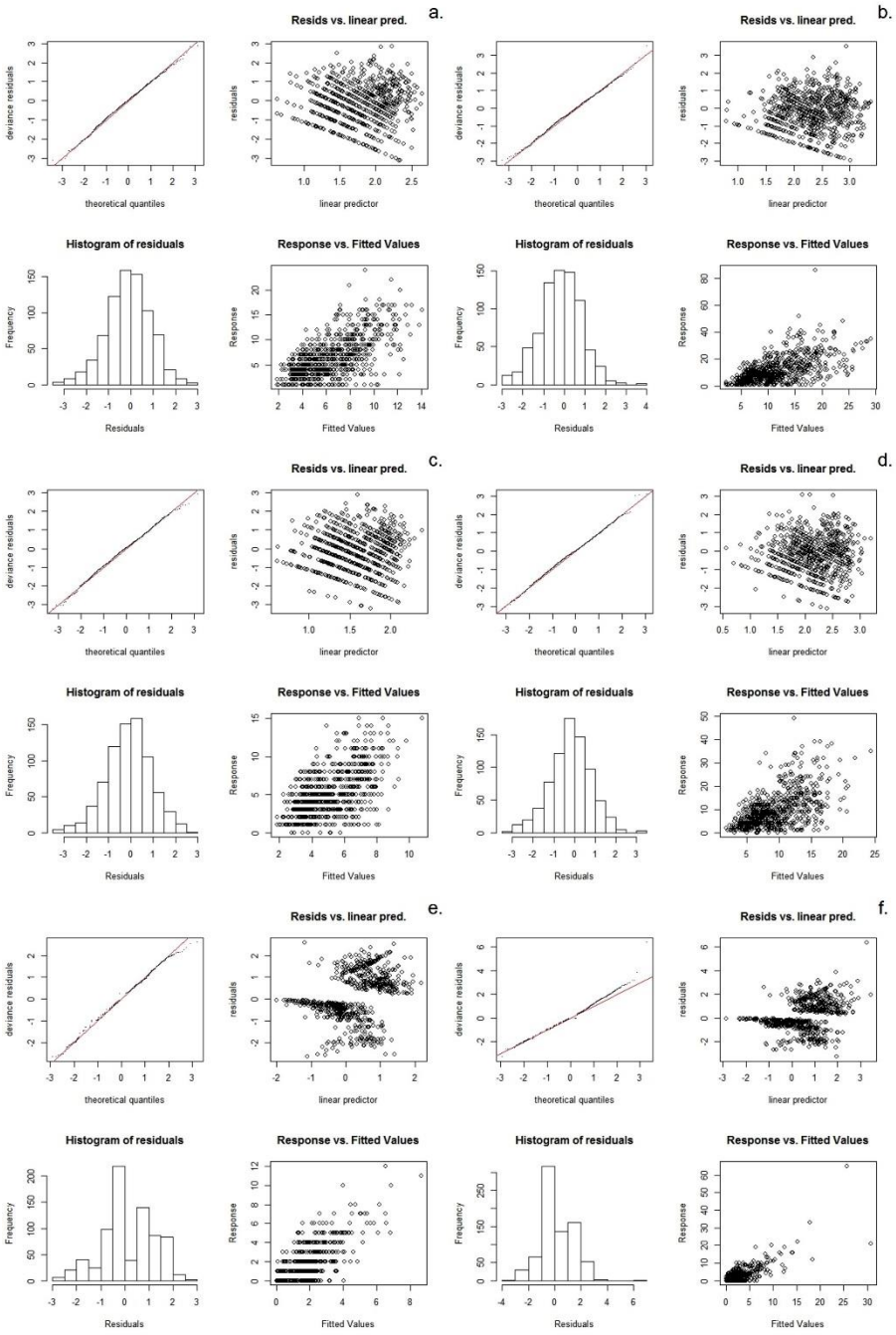

Figure S1. Diagnostic information of fitted GAMMs. Response variables (a) mean total species richness, (b) mean total abundance, (c) mean resident species richness, (d) mean resident abundance, (e) mean migratory species richness and (f) mean migratory abundance.

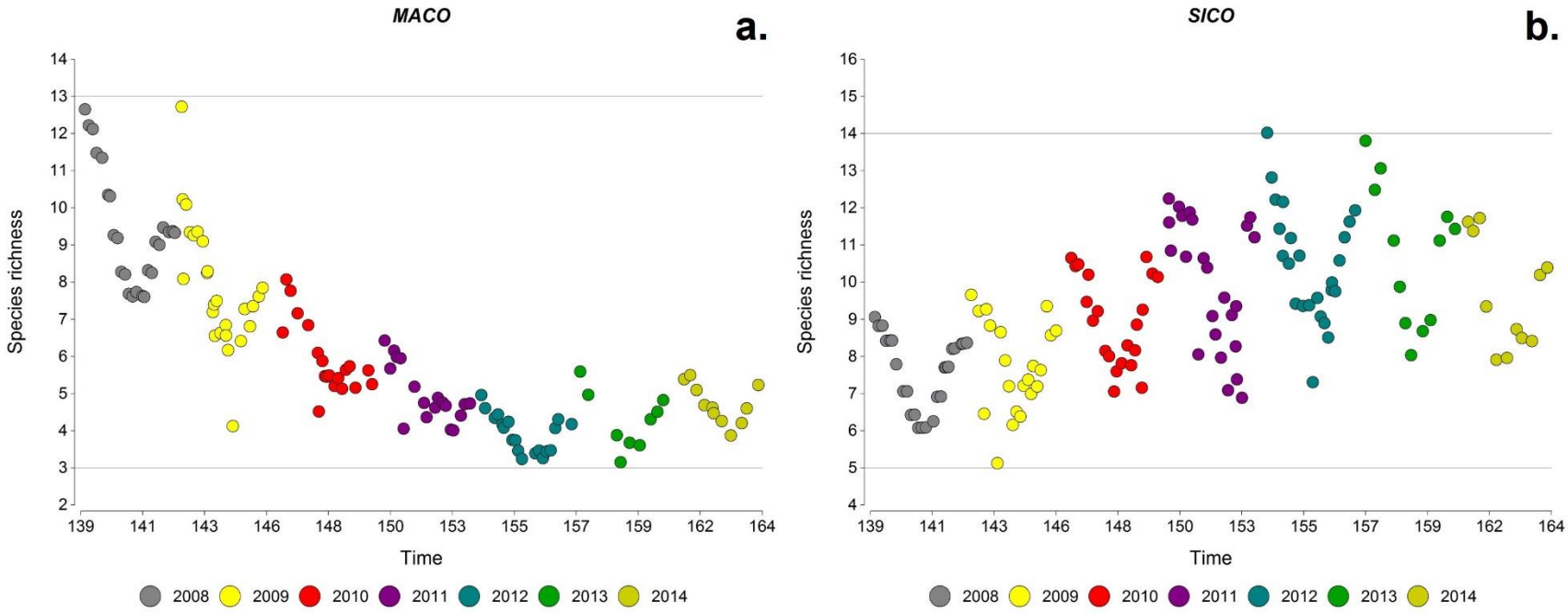

Figure S2. Predicted values of overall bird species richness. Where multi strata coffee agroforest (MACO) and simplified coffee agroforest (SICO).

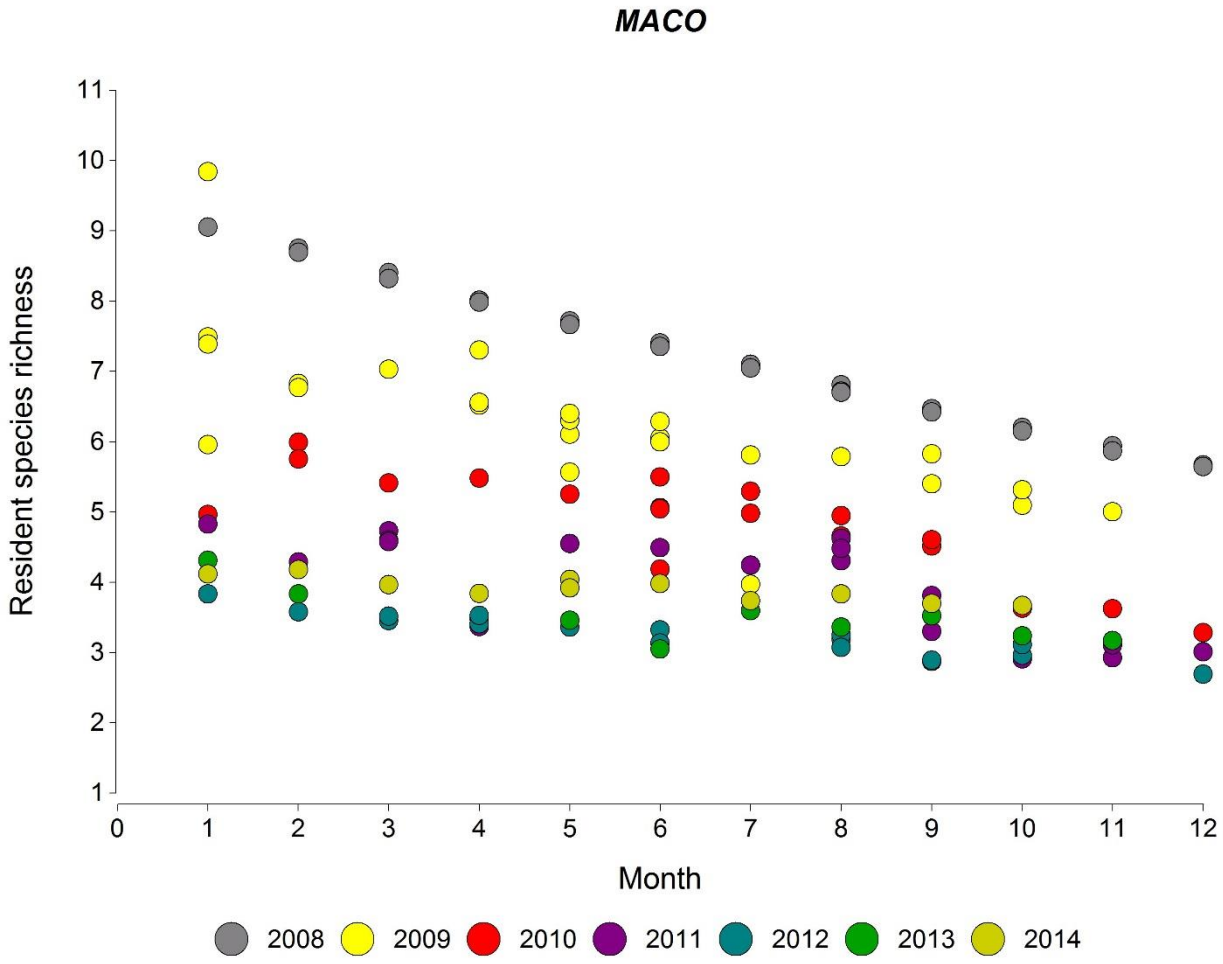

Figure S3. Montly predicted values of resident species richness. Where multi strata coffee agroforest (MACO).

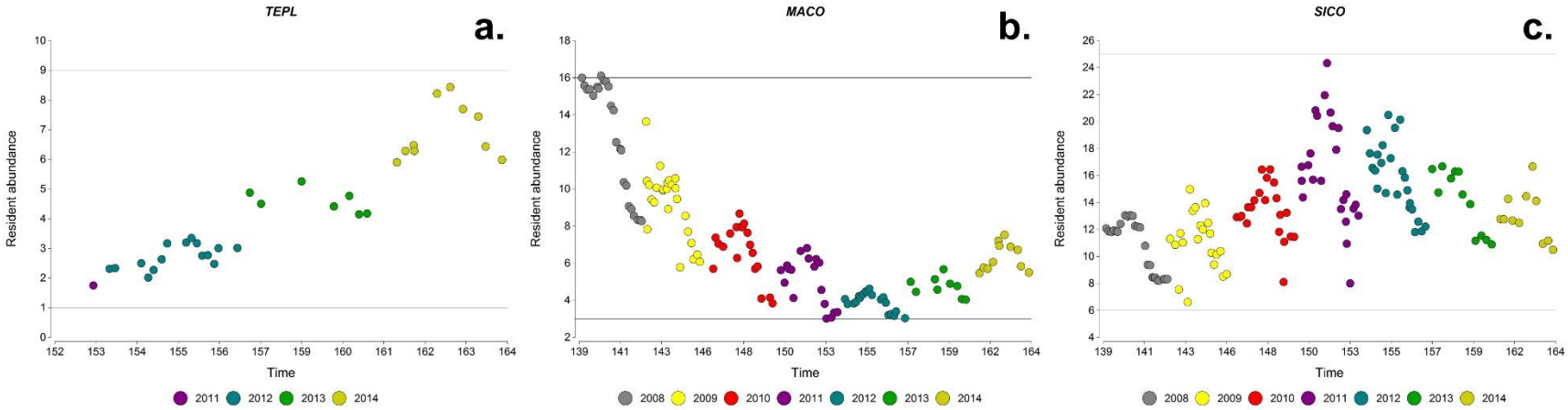

Figure S4. Predicted values of resident bird abundance. Where teak plantation (TEPL), multi strata coffee agroforest (MACO) and simplified coffee agroforest (SICO).

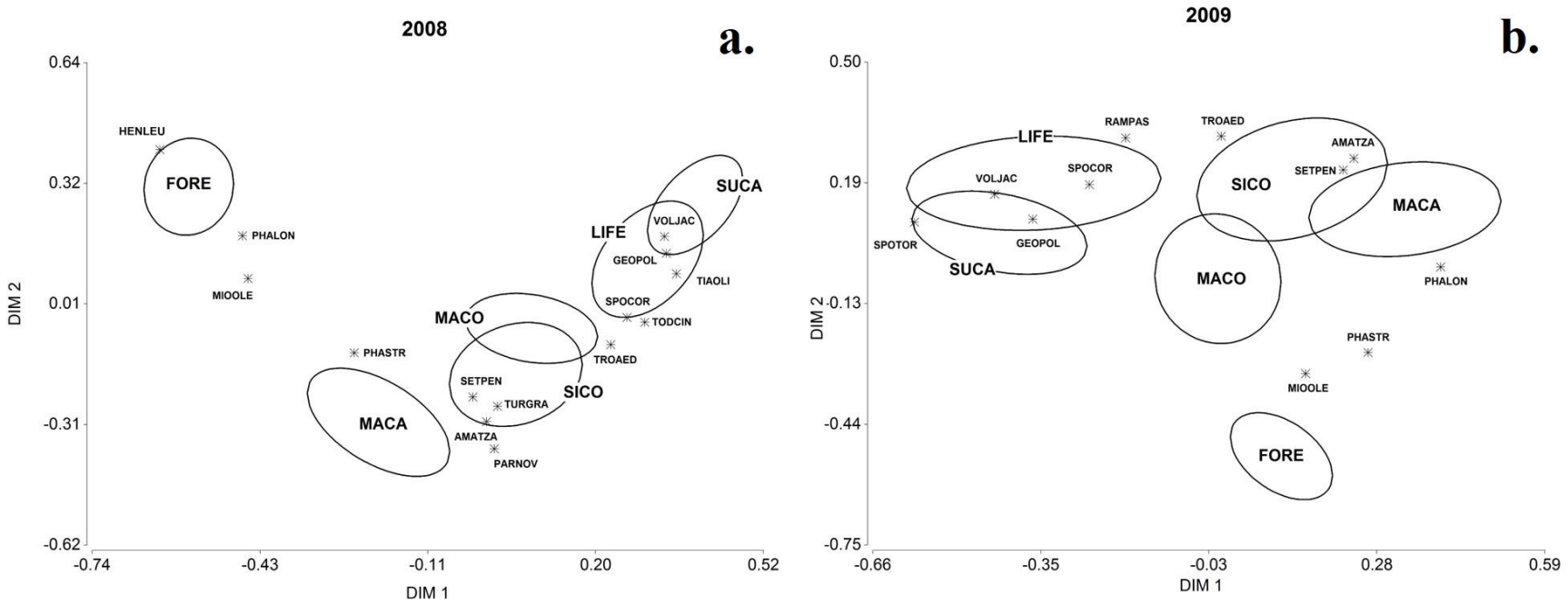

Figure S5. Ordination of land use types based on bird species composition for the years 2008 and 2009 where sugar cane (SUCA), multi strata agroforestry coffee (MACO), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA). Ellipses represent the confidence interval at 95% for each land use type. Asterisks represent bird species associated to land uses. Bird species six-letter code included in graphs, for species full name see Table S1.

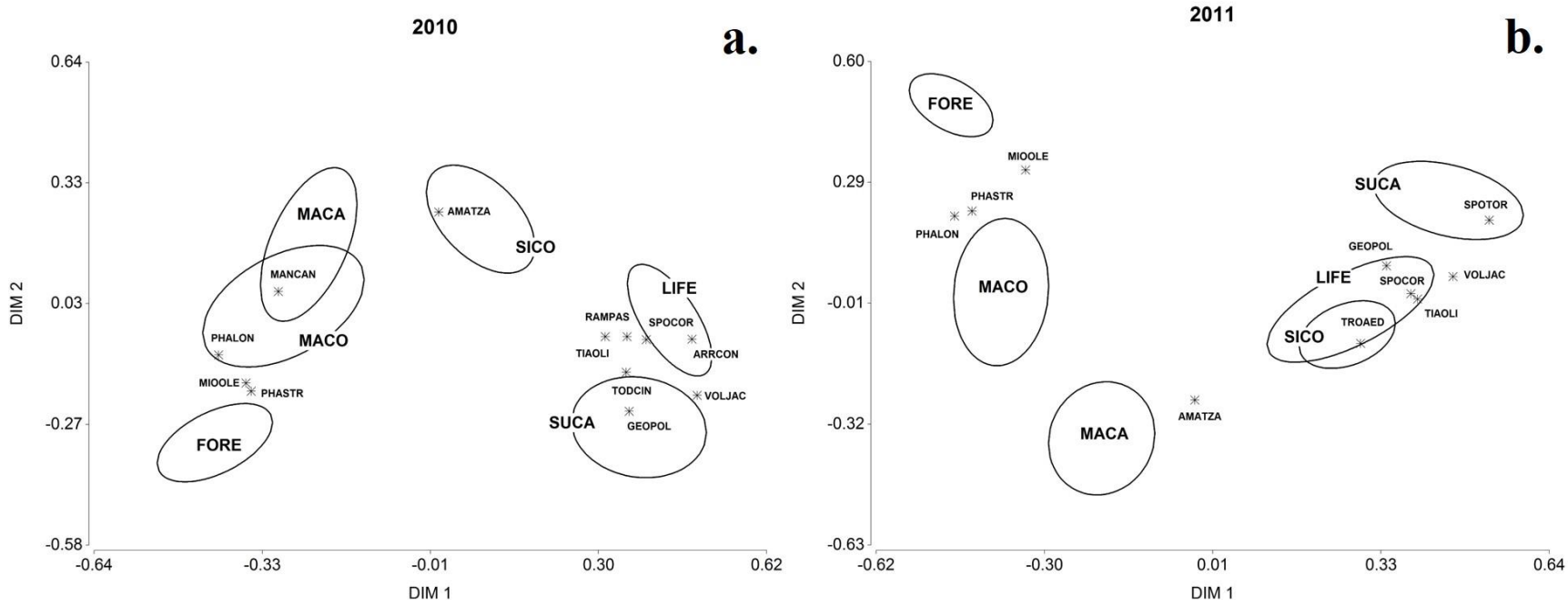

Figure S6. Ordination of land use types based on bird species composition for the years 2008 and 2009 where sugar cane (SUCA), multi strata agroforestry coffee (MACO), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), and multi strata cacao agroforest (MACA). Ellipses represent the confidence interval at 95% for each land use type. Asterisks represent bird species associated to land uses. Bird species six-letter code included in graphs, for species full name see Table S1.

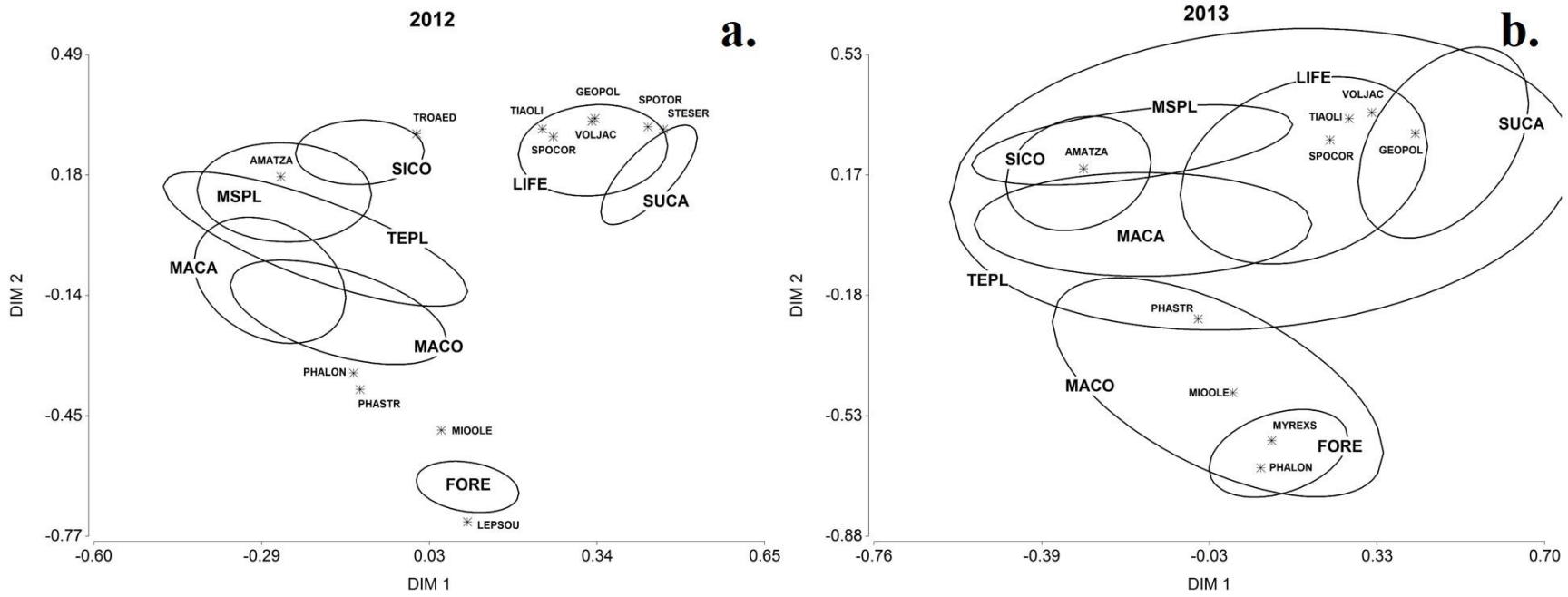

Figure S7. Ordination of land use types based on bird species composition for the years 2012 and 2013 where sugar cane (SUCA), multi strata agroforestry coffee (MACO), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), multi strata cacao agroforest (MACA), mixed species plantation (MSPL) and teak plantation (TEPL). Ellipses represent the confidence interval at 95% for each land use type. Asterisks represent bird species associated to land uses. Bird species six letter code included in graphs, for species full name see Table S1.

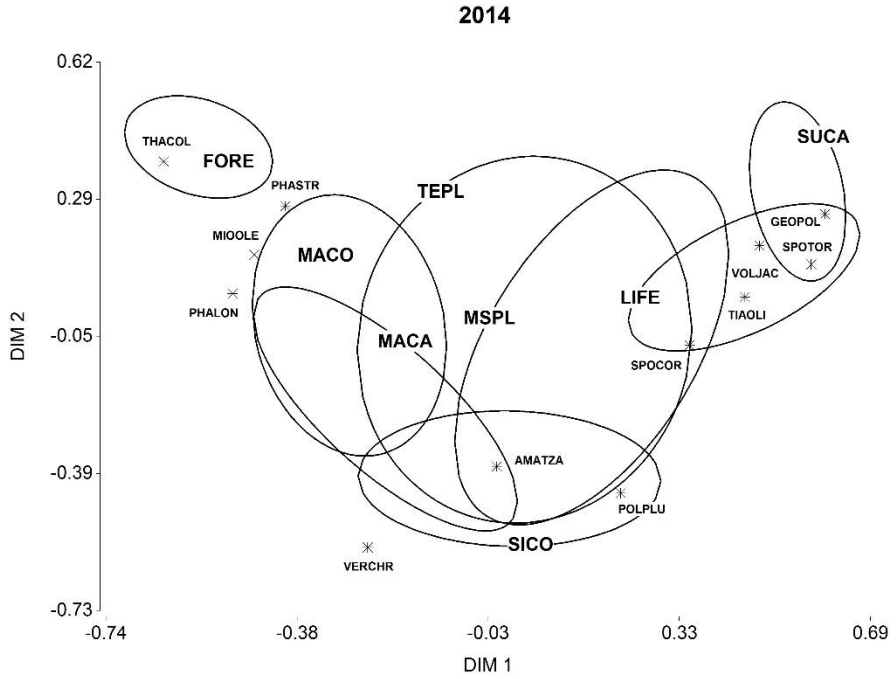

Figure S8. Ordination of land use types based on bird species composition for the year 2014 where sugar cane (SUCA), multi strata agroforestry coffee (MACO), simplified coffee agroforest (SICO), secondary mature forest (FORE), live fences (LIFE), multi strata cacao agroforest (MACA), mixed species plantation (MSPL) and teak plantation (TEPL). Ellipses represent the confidence interval at 95% for each land use type. Asterisks represent bird species associated to land uses. Bird species six letter code included in graphs, for species full name see Table S1.

Chapter 3: Bird functional diversity supports pest control services in a Costa Rican coffee farm

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Abstract

Understanding how species functional traits relate to the delivery of ecosystem services is essential to support on-going biodiversity conservation efforts. While much recent work has been conducted, relatively few studies relating functional ecology to ecosystem services has utilized field experiments, particularly for animal species. We used a functional diversity (FD) approach to study the effect of bird traits on the control of the coffee berry borer (*Hypothenemus hampei*) and the effect of canopy cover management on bird FD. We conducted an exclosure experiment to test the effect of bird FD on the difference of *H. hampei* infestation rates between coffee shrubs both exposed to, and excluded from bird foraging activity. We addressed the following questions: (1) is avian FD, at the plot level, a good predictor of *H. hampei* infestation? (2) do gleaner bird species contribute to the control of the pest? and (3) how does shade management affect avian FD? We found that (1) all four FD indices calculated using bird traits were significant predictors of *H. hampei* differences in infestation rates, (2) richness of gleaning bird species was also a significant predictor of differences in *H. hampei* infestation rates, and (3) the interaction between month and canopy cover management affects bird FD, however whether this affects delivery of the pest control

service remains unclear due to the particular biology of *H. hampei*. In revealing the connection between avian traits and the removal and potential control of *H. hampei*, our study highlights the importance of bird diversity persisting in agricultural landscapes, and the necessity of integrating bird conservation to foster healthy production systems.

Keywords: *Hypothenemus hampei*, coffee berry borer, Coffea arabica, exclosure, vertebrate, gleaner, biological control

1. Introduction

Coffee is one of the most important crops in tropical regions of the world. Coffee production is estimated to cover over 10 million ha (FAOSTAT 2015) of the 1.53 billion ha dedicated to cropland (38% of world land surface when added to pasture lands) (Foley *et al.* 2011). Coffee is considered one of the most important economic crops worldwide and one of the few so-called soft commodities (Ricketts *et al.* 2004; FAO 2007). In the American tropics, coffee is usually produced in agroforestry systems, making important contributions to biodiversity conservation in agricultural landscapes (Jha *et al.* 2014) and overlapping with important biodiversity conservation regions (Myers *et al.* 2000). Agroforestry coffee systems are particularly important for bird conservation (Greenberg *et al.* 1997a, b; Frishkoff *et al.* 2014). But the inverse is also true in that biodiversity can make important contributions to agricultural functions by delivering crucial ecosystem services like pollination (Klein *et al.* 2007; Kremen *et al.* 2007) and pest control (Milligan *et al.* 2016).

In coffee fields and other habitats, individual bird species and interactions among species are critical for supporting ecosystem functioning and the provision of multiple ecosystem services (Tilman *et al.* 1997; Zavaleta *et al.* 2010; Mouillot *et al.* 2013). Understanding how single or assemblages of species deliver ecosystem services is needed to decrease negative effects of agricultural production, as well as to elucidate the connection between ecosystem service based management and biological conservation (Wenny *et al.* 2011). Examples of biodiversity contribution to ecosystem services in coffee include carbon sequestration (Tumwebaze and Byakagaba 2016), pollination (Classen *et al.* 2014) and pest control (Kellermann *et al.* 2008; Johnson *et al.* 2010; Karp *et al.* 2013). These services are provided by different ecological mechanisms that range from single species effects (Jedlicka *et al.* 2011), to community or distance based effects (Ricketts 2004; Avelino *et al.* 2012; de la Mora *et al.* 2015), spilling over from forest (Blitzer *et al.* 2012), changing the habitat value of coffee plantation through agroforestry (Perfecto *et al.* 1996; Jha *et al.* 2014).

Understanding the mechanisms by which bird species deliver pest control services is particularly important as it directly benefits and is appreciated by farmers (Fremier *et al.* 2013). The importance of bird species in reducing arthropod pest densities has been well established in other agroecosystems (Greenberg *et al.* 2000; Perfecto *et al.* 2004; Borkhataria *et al.* 2006; Van Bael *et al.* 2008) with the magnitude of pest reduction ranging from 64 to 80% (Greenberg *et al.* 2000). This is particularly true for the coffee berry borer (*Hypothenemus hampei* (Ferrari), Coleoptera: Cucurlionidae) which can account for up to 50-100% losses if appropriate control measures are not implemented (Le Pelley 1968). *Hypothenemus hampei* is one of the most harmful and difficult to control coffee pests

worldwide (Damon 2000; Vega *et al.* 2009) (Fig. 1). *Hypothenemus hampei* is a small (~ 2 mm) beetle originating from Africa and now widely distributed across all major coffee producing regions of the world (Damon 2000; Vega *et al.* 2009). The complete *H. hampei* life cycle occurs within coffee berries previously colonized by inseminated females (Damon 2000). In optimal conditions, female *H. hampei's* may lay over 100 eggs within a single berry. Only female *H. hampei's* develop wings, fly and disperse, and are thus primarily responsible for pest dispersal (Damon 2000; Vega *et al.* 2009).

Recent studies specific to *H. hampei* have found that insectivorous bird species play an important role in controlling the beetle (Kellermann *et al.* 2008; Karp *et al.* 2013). Karp *et al.* (2013) emphasizes the contribution of adjacent habitat, (i.e. forests) in providing pest control through spill-over effects. However, questions remain about the effectiveness of remnant forests as supporters of *H. hampei* predators proving that more information is needed about the relationships between birds and *H. hampei* predation. These studies, for example did not examine the importance of bird traits in such control.

Functional traits allow for greater understanding of individual and collective contributions of avian diversity to ecosystem service provision. Functional diversity (FD) is key to understanding how species interactions translate into ecosystem functioning and service provision (Chapin *et al.* 2000; Diaz and Cabido 2001). The FD of a community allows us to study the value, range, distribution and abundance of traits possessed by species within these communities (Diaz and Cabido 2001). A functional trait is any measurable characteristic of any given individual. In the case of animal species, these traits can include morphological,

physiological, phenological or behavioral characteristics (Violle *et al.* 2007; Luck *et al.* 2012). The study of traits provide important insights into bird species ecological functions and thus delivery of ecosystem services (Flynn *et al.* 2009; Philpott *et al.* 2009). For instance, species that might be considered unimportant for pest control might be playing a critical role in the provisioning of this particular service (Mouillot *et al.* 2013). Additionally, basing analyses on species traits can help in assessing the resilience of maintaining ecosystem functions and services across time and space (Ricketts *et al.* 2004). Understanding the effect of bird traits in the removal of *H. hampei* is needed to promote appropriate biodiversity conservation practices in agricultural lands.

There are important agroecological questions related to the impact of biodiversity on ecosystem services. We address this gap by using a Functional Diversity approach to study the effect of avian traits in *H. hampei* control. We evaluated the effect of bird FD in *H. hampei* control by conducting an exclosure experiment to test the effect of bird FD on the difference of *H. hampei* infestation rates between coffee shrubs both exposed to, and excluded from bird foraging activity. We addressed the following questions: (1) is avian FD, at the plot level, a good predictor of *H. hampei* infestation? (2) do gleaner bird species richness, or gleaner diversity play a disproportionately large role in accounting for *H. hampei* removal? and (3) how does shade management affect avian FD? Although there have been a handful studies of avian diversity and *H. hampei* (Kellermann *et al.* 2008; Johnson *et al.* 2010; Karp *et al.* 2013) this is the first study of bird FD in coffee agroecosystems that includes both measures of avian FD and of a specific agroecosystem service, in this case, *H. hampei* removal.

2. Methods

2.1. Study site

The study was conducted on the Tropical Agricultural Research and Higher Education Center (CATIE) farm, located in the Turrialba region of Costa Rica, Central America (Fig. 2). The CATIE property has an area of 1036 ha, encompasses a diversity of productive systems, and is situated (lat 9°53' N, long 83°43' W) within the Caribbean watershed of Costa Rica at 600 m.a.s.l. corresponding to the very humid pre-montane forest ecological zone. The average annual rainfall is 2636 mm, with mean temperature of 22 °C and a relative humidity of 87% (CATIE meteorological station, *unpublished data*). Rainfall is almost evenly distributed throughout the year but usually decreases between February and April, with 121 mm of rainfall on average over those three months. The absence of a marked dry season has consequences on the coffee flowering pattern. Flowerings are repeated and multiple, spanning from December to May. These multiple flowerings are of low intensity, resulting in multiple fruit cohorts and multiple harvest rounds between July and December. Because of its continuity, this flowering pattern is favorable to *H. hampei* survival during the inter-harvest period or dry season and subsequent population growth (Baker 1984).

CATIE is one of the largest farms in the Turrialba valley combining different production activities such as coffee (*Coffea arabica* var. caturra) (85 ha), sugar cane (127 ha), pastures (121 ha), forests plantations and reforestation plots (208 ha), nurseries and small organic agriculture plots. Additionally, the farm also includes approximately 200 ha of secondary forest. The majority of CATIE coffee fields are simplified agroforestry systems associated with Poró (*Erythrina poeppigiana*), a leguminous nitrogen-fixing tree. Poró trees are used as the dominant source of shade and are extensively pruned twice a year with canopy

cover values that can range from 0-80% in relation to the pruning and regrowth. Only a couple of coffee fields are grown in association with nutmeg trees (*Myristica sp.*), with lines of pine trees (*Pinus sp.*) dividing adjacent coffee plots. Most coffee fields, except a few experimental plots, are managed conventionally by applying herbicides and insecticides with occasional applications (once a year) of endosulfan (organochlorine insecticide, Thiodan) in an attempt to control *H. hampei* infestations.

2.2. Exclosure experiment

Plant selection: on January 2013 we identified suitable coffee fields for an exclosure experiment. We generated randomly distributed points, using *ArcGIS* (ESRI, Redlands, CA, USA), restricted by two main criteria: (1) > 20 m from field edges and (2) > 150 m apart. We found ten random points meeting these criteria. At each point, we selected paired coffee shrubs 5 m apart. The shrubs were of similar height (1.5 m) and vigor in foliage and fruit load. One of the pair was randomly selected to be enclosed with a plastic mesh (20 mm mesh size). The mesh was small enough to exclude foliage-gleaning birds but large enough to allow insect movement.

Bored berries supplementation: to homogenize the initial *H. hampei* population, each of the twenty coffee shrubs were supplemented with 150 bored berries placed on a cloth mesh hanging at their base. These infested fruits were collected from the same or nearby coffee fields. Supplemental infestations were conducted twice, at the beginning of the experiment in January 2013 and in May 2013, corresponding with peak periods of *H. hampei* movement and colonization of new berries.

Hypothenemus hampei surveys: to estimate infestation density we randomly selected five branches (n=100 branches in total), from the middle to upper sections and counted total number of berries and total number of bored berries on each branch on a monthly basis. Branches on the lower portions were not selected to avoid biases via supplementation. From June to December we additionally collected and counted all ripe, healthy and bored berries. *Estimation of H. hampei availability*: we monitored *H. hampei* flying events and densities using Brocap® traps (PROCAFE, Santa Tecla, El Salvador, and CIRAD, Montpellier, France) which use a combination of methanol-ethanol (3:1 volume) proven effective in attracting and trapping *H. hampei* (Dufour and Frérot 2008). Two Brocap® traps were installed per study plot (Fig. 2c), with exclosure establishment, 20 m from paired coffee shrubs and > 40 m apart. We determined *H. hampei* flying events and densities by counting total number of individuals caught in traps every two weeks.

2.3. Predatory evidence

To obtain direct evidence of bird predation on *H. hampei*, we collected stomach content and faecal samples from bird species captured within our study plots. Once a month, between February to August 2013, we installed 5 to 8 mistnets (12 m x 2.5 m, 30 mm mesh size) in each study plot (Fig. 3) and targeted bird species based on three criteria: (1) potential *H. hampei* predators (Kellermann *et al.* 2008, Karp *et al.* 2013), (2) diet and foraging strategy and (3) size. Capture dates corresponded to those of peak *H. hampei* annual flying activity and thus highest availability for predation.

Stomach content and faecal samples: We obtained stomach content samples by administering an emetic (University of Idaho ACUC protocol #2012-20, CR Scientific

Passport # 04541). Our emetic selection was based on zero mortality (Diamond *et al*. 2007) in the application of *ipecac* (*Carapichea ipecacuanha*) in comparison to other emetics traditionally used (Poulin and Lefebvre 1995, Johnson *et al.* 2002). Our protocol used *syrup* form of *ipecac* and was administered using a pipette allowing delivery directly into the throat of birds. Individual doses were based on body mass following recommendations by Diamond *et al.* (2007). Individuals receiving the *syrup* were placed in temporary holding cages (30 x 30 cm) lined with a clean paper towel and covered by a dark cloth to reduce stress. Birds were left undisturbed for 10 to 15 min and then evaluated. After emesis was produced, birds appearing to be alert and in good condition were immediately released. Individuals showing stress signs were placed on different holding cages until recovery. Same day recaptures were immediately released without taking additional samples. Mortality rate was 1.89% (three individuals out of 159). Emesis and faeces samples were collected from the paper lining. All cages and instruments were cleaned before re-use, to prevent contamination. Additional faecal samples were collected from cloth bags used to transport birds from capture to processing sites; cloth bags were used only once to prevent sample contamination.

DNA analyses: DNA was extracted using QIAGEN mericond food kit following the manufacturer's standard protocol for 200 mg tissue. We modified this by adding 50 µl of Elution Buffer to elute DNA. Published borer-specific primers (Jaramillo *et al.* 2010) were used to amplify a 185 bp segment of mitochondrial DNA (Cytochrome Oxydase I or COI) in both faecal and emesis content. We used 5 µl of each extract. PCR was ran in 25 µl with 1 X Green GoTaq® Flexi Buffer, 2 mM MgCl2, 0.2 mM of each dNTPs, 0.25 mM of each primer, 1 unit of GoTaq® G2 Flexi DNA Polymerase (Promega), in a basic thermocycler (Biometra). PCR cycling protocols were 94 °C for 2 min followed by 40 cycles of 94 °C for 30 s, 55 °C

for 45 s, 72 °C for 1 min and a final extension of 72 °C for 10 min. Electrophoresis of 15 µl of PCR product in 1.5% agarose gel in TAE buffer (Tris-Acetate-EDTA) stained with ethidium bromide was completed to determine reactions success. Positive controls containing DNA of the target prey species and negative controls containing water instead of DNA were included in each PCR to check for amplification success and DNA contamination. The positive products were sequencing by Beckman Coulter Genomics in both the forward and reverse directions. Samples matching the reference database with 99% similarity confirmed presence of *H. hampei*. Microsatellites marker HKK2.2 (Gauthier 2010) were also used to detect the presence of *H. hampei* DNA in stomach extracts; we only used stomach content assuming DNA from these samples would be less degraded than DNA obtained from faeces. Amplification was performed with the Mastermix Qiagen kit in a 10 µl volume containing 1 X Qiagen Multilexe Master Mix (+Q), 0.2 µM of each primer and 3 µl of extract DNA. PCR steps consisted of an initial denaturation of 15 min at 94 °C; 35 cycles of denaturation for 30 s at 94 °C, 55 °C for 90 s, extension at 72 °C for 75 s and a 20 min final extension step. The analysis of PCR products are the same as described earlier except that a 10 µl volume was used. Size of expected fragments was around 150 bp. Size of all amplicon was compared with size of positive controls (DNA *H. hampei* template).

2.4. Canopy cover estimation

We used a spherical densiometer (Forestry Suppliers, Inc.; Model C) to estimate canopy cover in five different locations within our 25 m radius study plots. Measurements were taken once a month. Four different readings (north, west, south and east) were taken allowing estimation of average canopy cover per study plot per month.

2.5. Bird species composition and functional diversity

From February to November 2013, we conducted bird surveys on each study plot. Surveys consisted of recording all birds seen and heard in a 10 min period within a 25 m radius detection distance (Ruiz-Gutierrez *et al.* 2010). We constructed a bird-trait database using species identified within our 25 m radius excluding fly overs. Information from species caught in mistnets was excluded since captures were limited to a few months. We selected traits important to insectivory, including those used by Philpott *et al.* (2009) and Luck *et al.* (2012): (1) body mass, (2) preferred foraging location, (3) preferred habitat type, (4) preferred food type; plus additional morphological traits: (5) bill length, (6) bill length from tip to nares, (7) bill height, (8) bill width, (9) tarsus length, and (10) body length. Morphological traits were measured on specimens kept in the Costa Rica National Museum and University of Costa Rica collections. We measured a minimum of five specimens to obtain an average trait value; in cases of sexual dimorphism we measured five male and five female specimens. Traits related to foraging location, habitat and food type were obtained through a literature review (Stiles and Skutch 1989) and existing trait databases (Philpott *et al.* 2009, Flynn *et al.* 2009).

Functional diversity (FD) index calculation: we used traits from 67 bird species to calculate four multi-trait abundance-weighted indices: (1) functional richness (FRic); (2) functional evenness (FEve); (3) functional divergence (FDiv) (Villéger *et al*. 2008); and (4) functional dispersion (FDis) (Laliberté and Legendre 2010). These indices provide complementary FD and trait distribution information (Mouillot *et al.* 2005; Mason *et al.* 2005). FRic quantifies the amount of functional space occupied by species traits; extreme trait values are used in the construction of the convex hull bounding the possible trait values. FRic

values are not constrained, as the volume occupied by traits may change with the inclusion of additional larger trait values (Villéger *et al.* 2008). FEve quantifies the regularity in which community traits filled the multivariate space (uniformity of abundance distribution). FEve values are constrained between zero and one, and approach zero when abundance values are distributed unevenly amongst species or when functional distances (obtained from the minimum spanning tree calculation) between species are irregular (Mason *et al.* 2005, Villéger *et al.* 2008). FDiv quantifies the distribution of trait values relative to the "center of gravity" of the multivariate space occupied by those traits and weighted by their abundance; abundant species with larger trait values will increase FDiv values (Mason *et al.* 2005, Villéger *et al.* 2008). FDiv values are constrained between zero and one, "approaching zero when highly abundant species are very close to the center of gravity relative to rare species and unity when highly abundant species are very distant from the center of gravity relative to rare species" (p. 2295, Villéger *et al.* 2008). Finally, FDis calculates "the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species" (p. 304, Laliberté and Legendre 2010) and is hence a multivariate measure of trait dispersion. FDis values are not constrained.

2.6. Statistical analysis

We used Generalised Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs) (Zuur *et al.* 2009) to explore relationships among the response variables (i) bird species richness, (ii) bird abundance, and (iii) bird FD indices with the predictors (i) average canopy cover (CC), (ii) time of year (month) and (iii) their interaction, average CC was

declared as a co-variate. In all models, we assigned study plots as random effects. We used Poisson distribution in GLMMs for bird species richness and abundance; and LMMs for bird FD. In LMMs we modeled variance heterogeneity by including a function of specific variances for each study plot (R function varIdent). We evaluated errors lack of independence through autocorrelation diagnostic graphs (R autocorrelation functions acf and pacf). Estimation of parameters was conducted using Maximum Likelihood (ML) for GLMMs and Restricted Maximum Likelihood (REML) for LMMs.

We used Linear Mixed Models (LMMs) to test the effect of treatment (enclosed and non-enclosed) on the total number of bored berries. We used the natural logarithm of the total number of bored berries as a response variable, the total number of berries as a co-variate. Study plots were declared as random effects. Parameters were estimated via REML. Additionally, we used Generalised Additive Mixed Models (GAMM) (Zuur *et al.* 2009) to test the effect of bird species richness, bird species abundance, bird gleaning species, bird FD indices, month and their interaction on the difference of bored berries from non-enclosed minus enclosed coffee shrubs. The difference of total berry production from non-enclosed minus enclosed coffee shrubs was included as a co-variate. Study plots were declared as random effects. We used P-splines as smoothing functions for single factors and a tensor product for interactions. Single factors and their interactions were considered to be significant when $P < 0.05$. Analyses were performed with nlme, lme4 and mgcv R packages (version 3.1.2) using the implemented interface in *InfoStat* (Di Rienzo *et al.* version 2015).

FD indices were calculated using *F-Diversity* software (Casanoves *et al.* 2011). Prior to the calculation of indices, all trait values were standardized to a mean of 0 and a standard

deviation of 1. We used dummy variables to deal with categorical traits and species abundance as weights.

3. Results

3.1. Bird community

In total, we observed 2,187 birds belonging to 97 species and 35 families. The overall bird community varied in diet and residency status; with 25 species (26%) classified as exclusive insectivores; 31 (32%) classified as insectivores also feeding on small fruits, seeds and nectar; 27 (28%) not classified as insectivores (since invertebrates does not constitute its main food source) but known to include invertebrates in their diets; the remaining 14 species (14%) are not known to feed on invertebrates (Stiles and Skutch 1989). Insectivore species numbers varied annually due to migratory events with 13 species (13%) out of the 97 classified as neotropical migrants, 6 species (6%) having migratory and resident populations; and the remaining 78 species (81%) considered year-round residents. Out of the 2,187 total observed individuals; 1,016 (46%) belonging to 67 species were observed within the boundaries of our 25 m radius bird surveys (Fig. 2c). The ten most common bird species, within the 25 m radius, comprised 60% (n = 609) of the total, with *Troglodytes aedon*, the small insectivorous House Wren being the most common species (Table 1).

3.2. Relationships among bird species richness, bird species abundance and bird FD indices; and average canopy cover and time of year

Bird species richness and bird abundance were well explained by time of year. The variable month was significant at predicting species richness (χ^2 = 19.18, P = 0.0237, n = 10)

and abundance (χ^2 = 45.19, P < 0.0001, n = 10). We found significant effects from month and average percentage canopy cover interactions, for two of our four FD indices. Functional evenness (FEve) ($F_{10,80}$ = 5.51, P < 0.0001, n = 10) and functional dispersion (FDis) ($F_{10,80}$ = 2.67, P = 0.0072, n = 10) (Fig. 4); and a marginally significant effect from month for functional richness (FRic) ($F_{9,71}$ = 2.06, P = 0.0447; *mean* = 0.46 ± 2.11, n = 10) and functional divergence (FDiv) ($F_{9,71}$ = 2.03, P = 0.0478, *mean* = 0.77 ± 0.08, n = 10).

3.3. Relationships between bird community and flying coffee berry borer availability

Numbers of available flying *H. hampei* vary temporally. The highest concentrations of *H. hampei* flights, during 2013, occurred between February-April and November-December. Following peaks of *H. hampei* flying availability (March) all measures of the community (Fig. 5 a-c) generally increased, although magnitude differed. Density of flying *H. hampei* tended to be low during the months of June to October and showed different peaks throughout the year.

3.4. Relationships among infestation rates and bird FD indices

We found significantly higher *H. hampei* infestation rates in enclosed coffee shrubs relative to non-enclosed coffee shrubs ($F_{1,8}$ = 21.85, P < 0.0016, n = 20), results from co-variate total fruit was non-significant ($F_{1,8}$ = 2.60, P < 0.1458, n = 20) (Fig. S1). Infestation rates from enclosed shrubs varied between 5.5% and 78.3% (*mean* = 25.9% ± 21.3, n = 10) while non-enclosed shrubs showed lower infestation rates that varied between 6.2% and 27.8% (*mean* = 16.2% ± 6.7, n = 10). The total number of berries harvested was 20,226 and 29,667 from non-enclosed and enclosed coffee shrubs respectively. Non-enclosed coffee

shrubs showed a total infestation of 14.49% (2930 bored berries) while enclosed shrubs showed a total infestation of 20.98% (6224 bored berries). These numbers are higher than those found in Turrialba (Avelino *et al.* 2012; 56 bored berries per coffee tree on average) or those reported by the Costa Rican Coffee Institute in Turrialba (ICAFE 2015) in the same year (less than 8% of infestation), possibly due to the supplementation of bored berries in our study. Finally, we also found that the interaction among month and species richness, species abundance, and bird FD indices was a significant predictor of bored berries differences (Table 2, Fig. 6).

3.5. Evidence of predation

We found direct evidence of bird predation on *H. hampei* by identifying DNA of the borer in samples of bird stomach content and faeces. We collected a total of 262 samples from 25 bird species captured within the 25 m radius in our study plots (Fig. 2c). We analyzed 87 emesis samples and 154 faecal samples for a total of 241 analyzed samples. We positively identified the presence of *H. hampei* DNA in eight different samples belonging to four bird species, *Setophaga petechia* (3), *Empidonax alnorum* (2), *Troglodytes aedon* (2) and *Todirostrum cinereum* (1). It is important to highlight that *Troglodytes aedon* (n = 124), *Setophaga petechia* (n = 83) and *Todirostrum cinereum* (n = 49) are also listed within the ten most common bird species identified through surveys (Table 1). Three additional samples were labeled as "potential" as we were able to assign the DNA to the genus *Hypothenemus* but not to the species *hampei*. However, from our *H. hampei* surveys we are able to estimate that over 95% of beetles trapped in the Brocap® traps belonged to the species *H. hampei* (n = 49,892) which appears to be the dominant *Hypothenemus* species in our study plots. Finally,

out of the eight samples containing *H. hampei* DNA, six were emesis and two were faecal samples (Table 3).

4. Discussion

Turrialba's agricultural matrix is a mosaic landscape capable of sustaining avian communities with functional traits required for the control of important crop pests. Evidence of the importance of bird's traits is highlighted through the trait-based FD indices significance in predicting *Hypothenemus hampei* infestation rates. There is evidence that ants are important predators of this pest (Gonthier *et al.* 2013, Morris and Perfecto 2016), particularly in shaded coffee systems (Armbrecht and Gallego 2007) however we attribute differences in infestation rates to the bird community given that both enclosed and non-enclosed coffee shrubs were accessible to ant colonization thus providing equal opportunity to predate on *H. hampei*. Additionally, bats are also known to be important arthropod regulators in coffee systems (Williams-Guillén *et al.* 2008), however Karp *et al.* (2013) found bat contribution to be negligible compared to birds when addressing *H. hampei* predation. Our study region is embedded in an agricultural landscape dominated by pastures and sugar cane, nevertheless; avian predators of *H. hampei* were among the most common bird species found in our study plots. This finding highlights that common bird species persisting in agricultural landscapes, despite often being overlooked, may be playing a critical role (Borkhataria *et al.* 2012; Martin *et al.* 2012; Mouillot *et al.* 2013; Maas *et al.* 2015; Garfinkel and Johnson 2015) in the suppression of important agricultural pests such as *H. hampei*.

In addition to the species-level *H. hampei* predation, our results demonstrated that measuring different components of bird functionality provides additional understanding to

how changes in community assembly may influence trait availability and thus ecosystem service provision (Mouchet *et al.* 2010; Mouillot *et al.* 2011). For instance, fluctuations in the effect of bird FD on *H. hampei* suppression (Fig. 6) may be a result of avian community reorganizations (Van Bael *et al.* 2008) limiting its capacity to provide specific traits. Avian community reorganizations, on the other hand, may be driven by resource availability; i.e. via *H. hampei* short vulnerability periods and completion of its life cycle inside of coffee berries (Damon 2000) which proves effective biological and chemical control challenging.

Overall estimated values of bird functional evenness (FEve) indicated that a more even distribution of species trait abundances might have increase *H. hampei* predation. Considering that 86% of bird species detected within our study plots were insectivores, increasing the evenness of their abundance distribution suggests that traits from all of these insectivores might be having a positive effect in reducing *H. hampei* infestation (Table 2); possibly a consequence of interspecies competition. Barbaro *et al.* (2014) found similar results in a transcontinental experiment, in which results show that increases in FEve increased overall bird insectivory.

Both neotropical migratory (NM) and year-long resident bird species were identified as predators of *H. hampei* with an average infestation reduction of 10%. Two NM species (Yellow Warbler, *Setophaga petechia* and Alder Flycatcher, *Empidonax alnorum*) and two yearlong resident bird species (House Wren, *Troglodytes aedon* and Common-Tody Flycatcher, *Todirostrum cinereum*) were positively identified as *H. hampei* predators (Table 3). Our results agree with Karp *et al.* (2013) in the identification of the Yellow Warbler as *H. hampei* predator in coffee systems in Costa Rica. Furthermore, DNA evidence collected from an aerial hawking species/flycatcher (*Empidonax alnorum*) suggests that both flycatchers and

gleaners might be important in the suppression of *H. hampei*. Actual contribution of resident and NM insectivorous bird species may be greater than what we are able to capture with our exclosure experiment given that exclosures only allow us to test hypotheses relating to *H. hampei* individuals removed directly from coffee shrubs (walking on coffee branches, waiting to or starting to bore berries) since flying *H. hampei* individuals could potentially colonize berries either in the enclosed or non-enclosed shrubs. These findings call for further research focusing on the importance of insectivorous bird species, particularly gleaners (Table 2) in the consumption of *H. hampei*, especially during dispersal and post-dispersal events.

Identification of NM and resident bird species as *H. hampei* predators brings attention to the importance of functional redundancy in the control of this and other agricultural pests. Functional redundancy acting as an insurance of this particular ecological function (Flynn *et al.* 2009; Luck *et al.* 2012). We found that even when species richness fluctuated, bird FD indices remained relatively stable throughout the year demonstrating redundancy of traits (Flynn *et al.* 2009) necessary for *H. hampei* predation. In our study plots, peak availability of flying *H. hampei* overlap with presence of NM (Fig. 5a); and even though there are fewer species, compared to residents, their contribution in number of individuals was far from trivial. Kellermann *et al.* (2008) demonstrated the importance of NM in the suppression of *H. hampei* through a similar exclosure study conducted in Jamaica, which found significantly higher *H. hampei* infestation rates in coffee shrubs excluded from bird activity and identified 17 bird species as potential *H. hampei* predators, 73% of which were neotropical migrants. Similarly, Van Bael *et al.* (2008) found that neotropical migrants were important in the reduction of overall arthropod densities.

Biodiversity friendly management practices within agricultural landscapes are crucial for the persistence of bird species and bird mediated ecosystem services. In our study, differences in bored berries were well predicted by the interaction between bird FD indices and month (Fig. 6). This brings attention to potential effects of farm management (Greenberg *et al.* 1997a; Kellermann *et al.* 2008) for both bird conservation and bird mediated pest control services (Whelan *et al.* 2008, Wenny *et al.* 2011, Sekercioglu 2012). In the Turrialba valley, for instance, pruning is an important activity conducted at least twice a year to boost coffee productivity and yield (Barradas and Fanjul 1986) and it has been demonstrated that intensity and timing of these management activities might have a direct impact on the bird species communities (Greenberg *et al.* 1997a). For example, Gras *et al.* (2016) found using exclusion studies that cacao yield may fluctuate between 100 and 800 kg ha^{-1} $year^{-1}$ as a result of ant and bird communities providing pest control services being affected by shade-tree management. Finally, in our study most bird species observed are fairly common however, we do not know anything about the condition of their populations or how farm and landscape management decisions are or might be affecting their persistence and thus the provision of critical services such as pest control.

5. Conclusion

The importance of bird species functional traits in suppressing *H. hampei* is demonstrated in our study by significantly higher infestation rates (up to 50% higher) in coffee shrubs that were isolated from bird foraging activity. We provided evidence that the Turrialba landscape is capable of sustaining bird species of importance for the provision of pest control services. However, farm management as well as management of landscape forest

elements (Karp *et al.* 2013) may be critical to secure persistence of such bird species. Better understanding of bird species role in the provision of ecosystem services calls for further research focusing on multiple service provision (Mouillot *et al.* 2011) and bird FD redundancy and complementarity (Flynn *et al.* 2009; Philpott *et al.* 2009) between resident and migratory species. Additionally, further explorations of molecular biology techniques allowing quantification of the magnitude of the pest control provided, as well as identification of key bird species for *H. hampei* suppression (Maas *et al.* 2015) are important research gaps that need to be filled in order to support bird conservation efforts within coffee dominated agricultural landscapes.

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Figure Legends

Fig. 1. (a) Ripe and green coffee fruits bored by *Hypothenemus hampei* (Coffee berry borer); (b) *H. hampei* individual compared to the size of a coffee fruit; (c) coffee fruit damaged by *H. hampei* activity compared to a normal coffee fruit. Figure B and C by Camilla Zanzanaini.

Fig. 2. Location and design of pest-control experiment in Turrialba, Costa Rica; all data were collected during 2013. (A) General study area location, at the country level; (B) CATIE farm, legend include all major landuses, black dots represent location of study plots (n = 10) within coffee fields; (C) Experimental design established on each of the study plots, squares at the center indicate position of enclosed (gray) and non-enclosed (white) coffee shrubs, inverted triangles on sides represent Brocap® trap locations, small circle at center represent bird survey locations, stars represent canopy cover measurements and outermost circle represents area covered by bird surveys (25 m radius) and where bird trapping was conducted.

Fig. 3. Photograph depicting a mist net set up between lines of coffee shrubs in a simple agroforestry coffee plot. Mist net installation includes the use of aluminum poles on each side to hold mist net in place, poles are anchored to the ground using rope.

Fig. 4. Interaction between average percentage canopy cover and month was significant at predicting changes in bird functional evenness and dispersion. (a) Shows interaction between average percentage canopy cover and month for functional evenness (FEve) (mean = 0.71 ± 0.14) and (b) functional dispersion (FDis) (mean = 1.63 ± 0.88).

Fig. 5. (a) Mean number of available *Hypothenemus hampei* individuals relative to resident and migratory bird species, (b) insectivorous and gleaner bird species; lines at the center of graphs (a) and (b) show time of year where neotropical migrants were absent (May 30th to August 24th) and gray coloring show peaks of flying *H. hampei* availability. "Date" displayed on the "x" axis in figures (a) and (b) corresponds to sampling dates where broca traps were collected and bird surveys were conducted. Graph (c) shows average values of bird FD indices throughout the year, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis), bars shows standard error.

Fig. 6. Bird species richness, bird species abundance and bird FD indices significantly reduced *Hypothenemus hampei* infestations in a Costa Rican coffee plantation. Graphs show predicted values of bored berries differences estimated by bird FD indices and month interaction. Negative values indicate higher *H. hampei* infestation in enclosed coffee shrubs, hence higher *H. hampei* removal in non-enclosed coffee shrubs. Color scheme show intensity of infestation, darker coloring indicate higher *H. hampei* infestation in non-enclosed shrubs. For instance, estimated values of bird functional richness (FRic) during May indicates greater *H. hampei* removal as FRic values increase; functional evenness (FEve) estimates indicate

that a more even species abundance distribution (approaching unity) predicts higher infestation rates in enclosed shrubs and thus higher *H. hampei* predation in non-enclosed shrubs; functional divergence shows no effect (straight lines) and functional dispersion shows that greater trait dispersion reduces effectiveness of *H. hampei* control.

Fig.1.

Fig. 2.

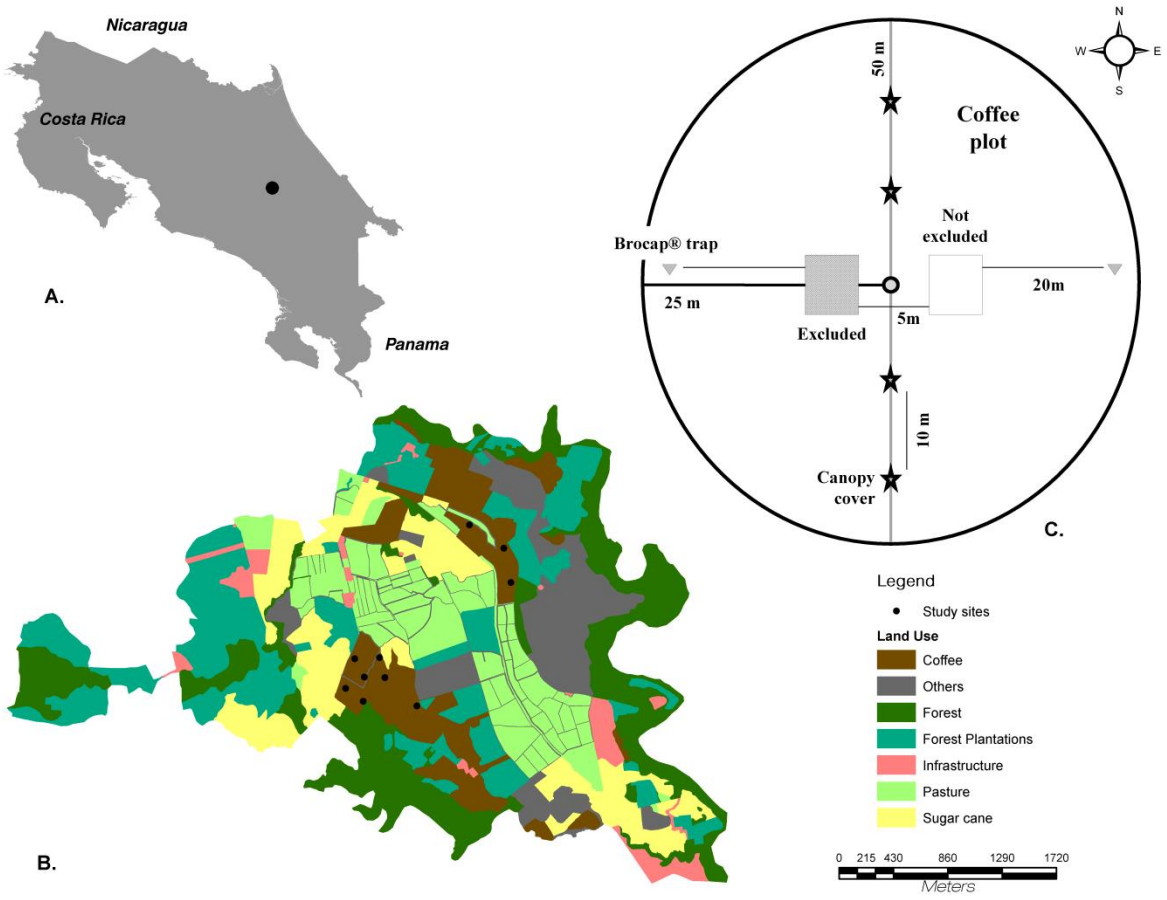

Nicaragua
Costa Rica
Panama
A.
B.
C.
N
W
E
S
50 m
Coffee plot
Not excluded
Brocap® trap
25 m
Excluded
5m
20m
10 m
Canopy cover
Legend
Study sites
Land Use
Coffee
Others
Forest
Forest Plantations
Infrastructure
Pasture
Sugar cane
0 215 430 860 1290 1720
Meters

Fig.3.

Fig. 4.

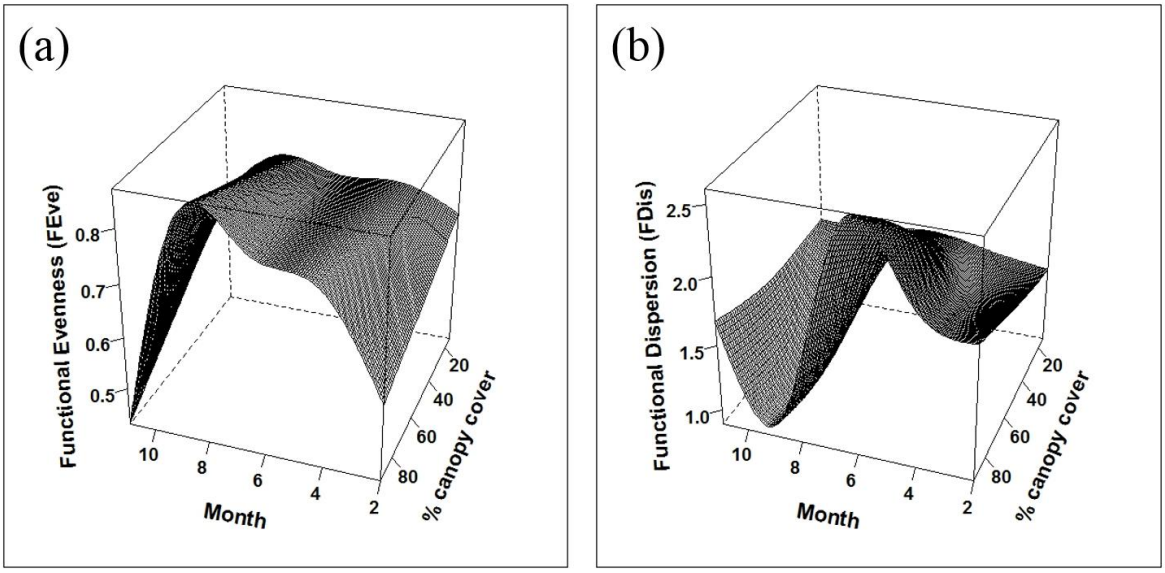

(a)
Functional Evenness (FEve)
0.8
0.7
0.6
0.5
10
8
6
4
2
Month
20
40
60
80
% canopy cover
(b)
Functional Dispersion (FDis)
2.5
2.0
1.5
1.0
10
8
6
4
2
Month
20
40
60
80
% canopy cover

Fig. 5.

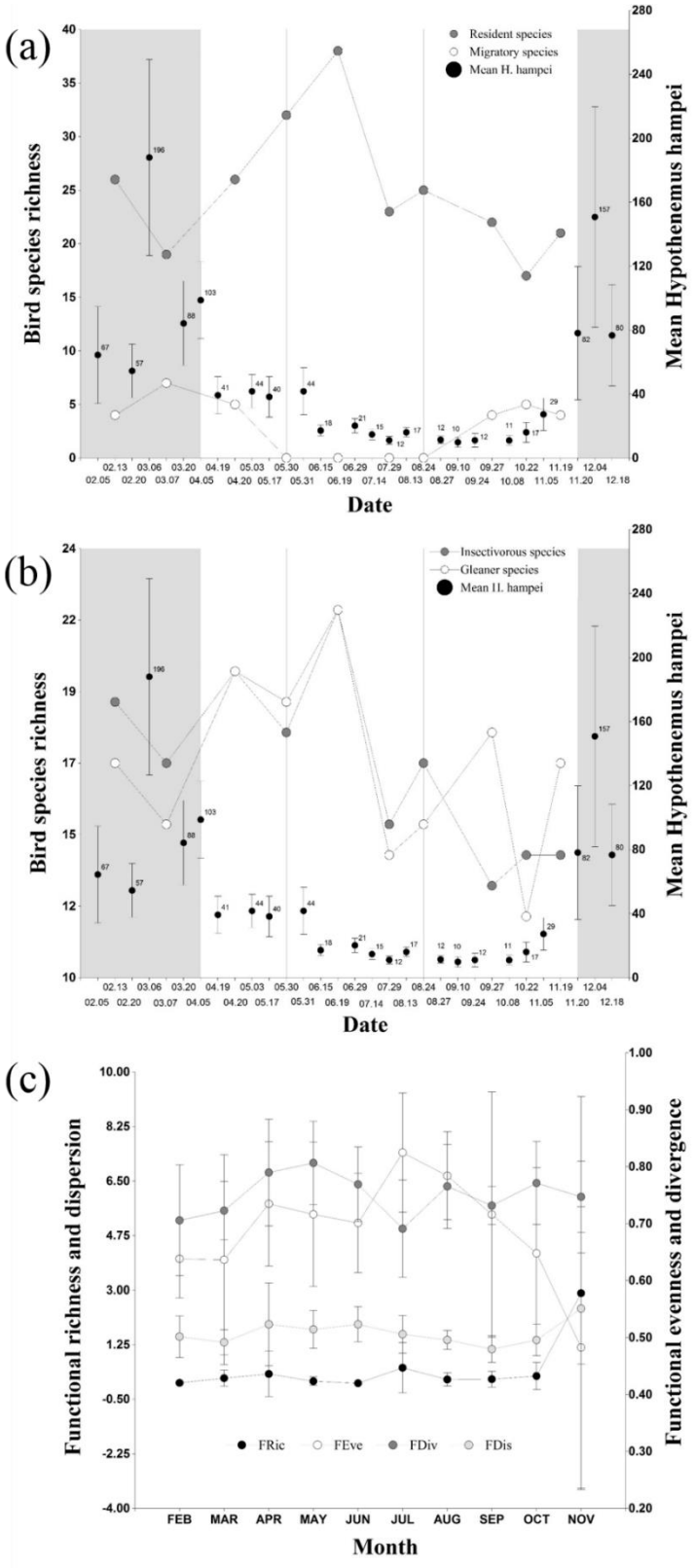
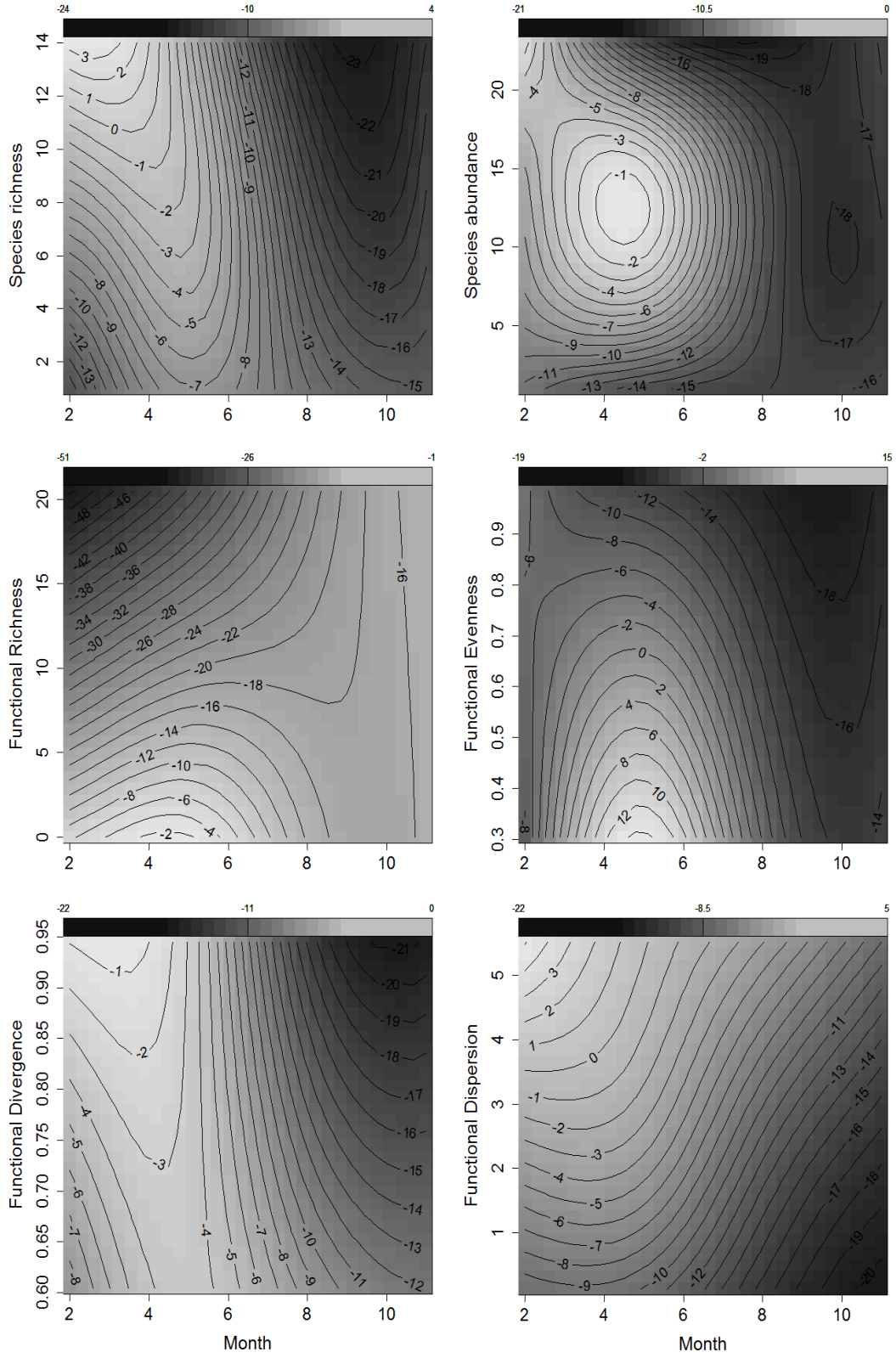

(a)
Resident species
Migratory species
Mean H. hampei
Bird species richness
Mean Hypothenemus hampei
Date
(b)
Insectivorous species
Gleaner species
Mean IL hampei
Bird species richness
Mean Hypothenemus hampei
Date
(c)
FRic
FEve
FDiv
FDis
Functional richness and dispersion
Functional evenness and divergence
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
Month

Fig. 6.


Species richness
Species abundance
Functional Richness
Functional Evenness
Functional Divergence
Functional Dispersion
Month
Month

Tables

Table 1

Ten most common bird species detected within the 25 m radius boundary of our bird surveys. Bird surveys were conducted from February to November 2013 including periods of spring (February – April) and fall migration (August – November). Status refers to whether the species are considered all year residents (R) or Neotropical migrants (NM); status classification follows the "Official List of the Birds of Costa Rica", annually updated and published by the Costa Rican Ornithological Association (AOCR).

Family	Feeding guild	Status	Latin name	English name	Total
Troglodytidae	Insectivore/gleaner	R	*Troglodytes aedon*	House Wren	124
Parulidae	Insectivore/gleaner	NM	*Setophaga petechia*	Yellow Warbler	83
Trochilidae	Nectarivore	R	*Amazilia tzacatl*	Rufous-tailed Hummingbird	81
Emberizidae	Granivore	R	*Sporophila corvina*	Variable Seedeater	78
Polioptilidae	Insectivore/gleaner	R	*Polioptila plumbea*	Tropical Gnatcatcher	72
Tyrannidae	Insectivore/gleaner	R	*Todirostrum cinereum*	Common Tody-Flycatcher	49
Emberizidae	Granivore	R	*Tiaris olivaceus*	Yellow-faced Grassquit	38
Hirundinidae	Insectivore	R, NM	*Stelgidopteryx serripennis*	Northern Rough-winged Swallow	34
Parulidae	Insectivore/gleaner	NM	*Setophaga pensylvanica*	Chestnut-sided Warbler	25
Emberizidae	Granivore	R	*Volatinia jacarina*	Blue-black Grassquit	25

Table 2

Effects of bird species and bird functional diversity indices on *H. hampei* infestation. The symbol ":" indicates interaction between month and each of the predictor variables. Results from ten study sites (pair treatments per study site).

Response variable	Predictor variable	R^2 (adj.)	Month:predictor variable		Difference total berry production (co-variate)	
			F-value	P-value	F-value	P-value
Difference of bored berries from non-enclosed minus enclosed coffee shrubs	Total bird species richness	0.668	2.775	0.0086	10.003	<0.0010
	Gleaner bird species	0.717	3.610	0.0004	10.702	<0.0010
	Gleaner + Nectarivore bird species	0.704	5.596	<0.0010	13.844	<0.0010
	All insectivore bird species (gleaners and non gleaners)	0.702	3.969	<0.0010	12.221	<0.0010
	All insectivore (gleaners and non gleaners) + nectarivore bird species	0.697	2.824	0.0035	10.009	<0.0010
	Bird species abundance	0.673	2.531	0.0121	10.368	<0.0010
	Functional Richness (FRic)	0.656	3.522	0.0048	9.481	<0.0010
	Functional Evenness (FEve)	0.670	3.333	0.0028	9.868	<0.0010
	Functional Divergence (FDiv)	0.654	2.962	0.0099	9.526	<0.0010
	Functional Dispersion (FDis)	0.655	3.206	0.0079	10.237	<0.0010

Table 3

Bird species identified as predators and as potential predators of *Hypothenemus hampei*. All species are insectivores and with the exception of the Alder Flycatcher all species are also considered gleaners. Status refers to whether the species are considered all year residents (R) or Neotropical migrants (NM); status classification follows the "Official List of the Birds of Costa Rica", annually updated and published by the Costa Rican Ornithological Association (AOCR).

Latin name	English name	Status	Feeding guild	Collection date	Sample type	DNA test	
						Cox1	Micro satellite
Setophaga petechia	Yellow Warbler	NM	Insectivore/gleaner	March 16	Stomach content	Positive	----
				March 18	Faeces	Positive	----
				April 10	Stomach content	----	Positive
				April 22	Stomach content	Potential	----
Setophaga pensylvanica	Chestnut-sided Warbler	NM	Insectivore/gleaner	March 19	Stomach content	Potential	----
Empidonax alnorum	Alder Flycatcher	NM	Insectivore/air hawker	May 02	Stomach content	----	Positive
				May 10	Stomach content	Positive	----
Troglodytes aedon	House Wren	R	Insectivore/gleaner	May 24	Stomach content	----	Positive
				May 27	Faeces	Positive	----
Todirostrum cinereum	Common Tody-Flycatcher	R	Insectivore/gleaner	May 28	Stomach content	Potential	Positive
Vireo flavoviridis	Yellow-green Vireo	MS	Insectivore/gleaner	June 05	Stomach content	Potential	----

Supplementary Information

Figure S1. Effect of treatment on the total number of bored berries from enclosed and non-enclosed coffee shrubs. Bars show errors.